

LOWER CARBONIFEROUS CONODONT FAUNAS FROM THE EASTERN MENDIPS, ENGLAND

by MALCOLM BUTLER

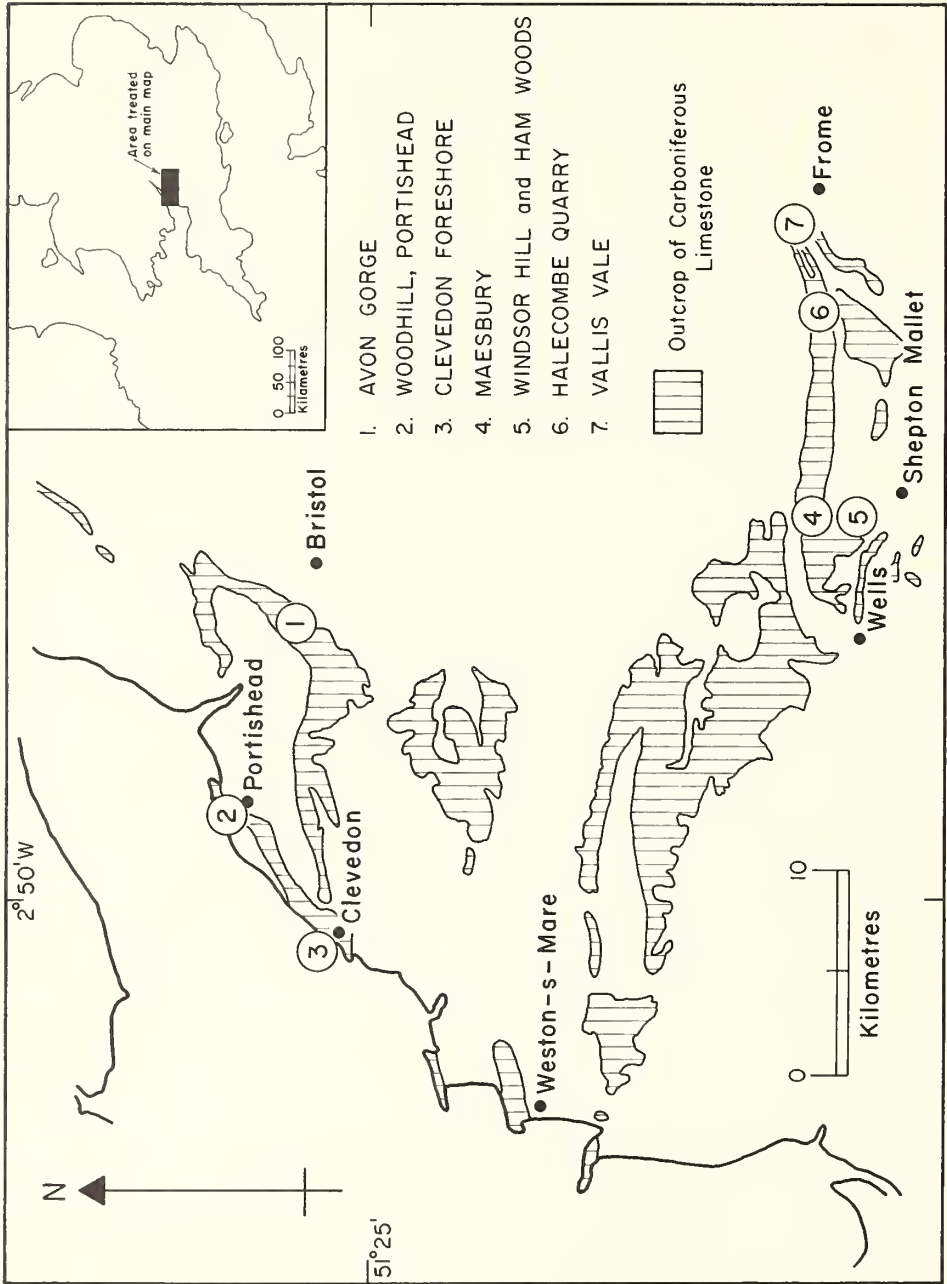
ABSTRACT. In the Mendip Hills, the lower part of the Carboniferous Limestone succession (the Lower Limestone Shale and Black Rock Groups) extends to greater thickness than is found in the Avon Gorge at Bristol. Conodont faunas from this range of the Mendip succession are described here. A distinctive lag-type deposit occurs low in the Lower Limestone Shale Group. Faunas below this lag (with *Patrognathus*, *Pseudopolygnathus dentilineatus*, *Polygnathus symmetricus*) cannot yet be dated precisely. Above, faunas with *Siphonodella*, *Elictognathus*, and *Gnathodus* correlate with those known from the late Kinderhookian of the U.S.A. and probably represent the range of the upper *Siphonodella crenulata*-Zone of Germany. Higher, in the middle part of the Black Rock Group, faunas typical of the German *anchoralis*-Zone appear. Particular interest attaches to the occurrence of *Scaliognathus anchoralis*, *Dollymae bouckaerti*, *Pelekysgnathus bultyncki*, and related forms. These compare closely with faunas recently described from Tn 3c in Belgium. None of the *anchoralis*-Zone species are known from the Avon Gorge succession, which is considered to be incomplete.

THE Carboniferous Limestone of the Bristol area provided the evidence on which Vaughan (1905) based his scheme of coral-brachiopod zones. More recently Kellaway and Welch (1955) have erected a series of lithological units for the Carboniferous Limestone of this area, intended to supersede Vaughan's zones. Neither of these schemes enables correlation to be made on anything more than a local scale. In an attempt to correlate on an international scale, Rhodes, Austin, and Druce (1969) studied the conodont faunas of the Avon Gorge section. However, these authors failed to recover certain important species of conodont, in particular the indices of the *anchoralis*-Zone (Bischoff 1957; Voges 1959, 1960).

Workers using both Vaughan's (1905) zones (e.g. Welch 1932) and the lithological units of Kellaway and Welch (1955) have noted that the strata near the top of the Black Rock Group (Z to C₁) thicken southwards from Bristol into the Mendips (see Kellaway and Welch 1955, pl. 1). It was decided to sample the Lower Limestone Shale and Black Rock Groups in the eastern Mendips to test the possibility that since the succession is thicker there, it might also be more complete, and might therefore produce conodont faunas which are not available in the Avon Gorge.

The sedimentary petrology of the sections sampled for conodonts has been studied in detail, and in addition a brief study has been made of the nature of equivalent levels in the Avon Gorge. The results of these investigations are considered elsewhere (Butler 1972). The sections were divided into sedimentological units, a brief description of each being given in text-figs. 3 to 10, along with details of sampling localities and sample numbers.

In the eastern Mendips the best section in the Lower Limestone Shale Group is that seen in the disused railway cutting at Maesbury (ST 606 475). Here the upper two-thirds of the Group are exposed, together with the transition to the overlying Black Rock Group (Green and Welch 1965). The lower and middle parts of the



TEXT-FIG. 1. Locality map, showing outcrop of the Carboniferous Limestone in the Bristol-Mendip area.

Black Rock Group are seen in disused quarries at Windsor Hill and Ham Woods (ST 615 452) and the middle and upper parts of this group are well exposed in a working quarry at Halecombe (ST 702 475). These sections were sampled systematically for conodonts, 2-kg samples being taken at 3-metre intervals. In addition a number of samples were taken from the middle and upper parts of the Black Rock Group in Vallis Vale (ST 755 490). This section is likely to provide a more permanent record than Halecombe Quarry, which is being actively worked. Isolated samples were also taken from Lower Limestone Shale Group exposures at Portishead (ST 465 775), Clevedon (ST 402 718), and Asham (ST 717 463) and from the Palate Bed in the Avon Gorge (ST 555 746). Faunal lists for these samples are given in an appendix, and the forms recovered are not treated systematically.

Conodont occurrence charts are given in text-figs. 3 to 10. 167 samples were processed and yielded 5324 identifiable specimens. 2491 of these are 'bar' forms. Yields per sample averaged 36 specimens in the Lower Limestone Shale Group and the lower and middle parts of the Black Rock Group. Certain samples gave relatively high yields, over 500 in one case (HW 18). Yields were especially poor in the upper part of the Black Rock Group (unit br 4), only three samples producing conodonts, and in this part of the succession samples were processed from 6-metre intervals only. Samples whose number bears a suffix 'a' come, in each case, from a level $1\frac{1}{2}$ metres above the preceding sample (e.g. HW 18a came from $1\frac{1}{2}$ metres above HW18). Duplicate samples were processed in a number of cases. None showed any marked differences from what was found in the first sample. Acetate peels were made of all rocks sampled for conodonts. The peels, bearing sample numbers, are stored in the Geology Museum, University of Bristol. There is no clear evidence of any link between conodont abundances and particular lithologies.

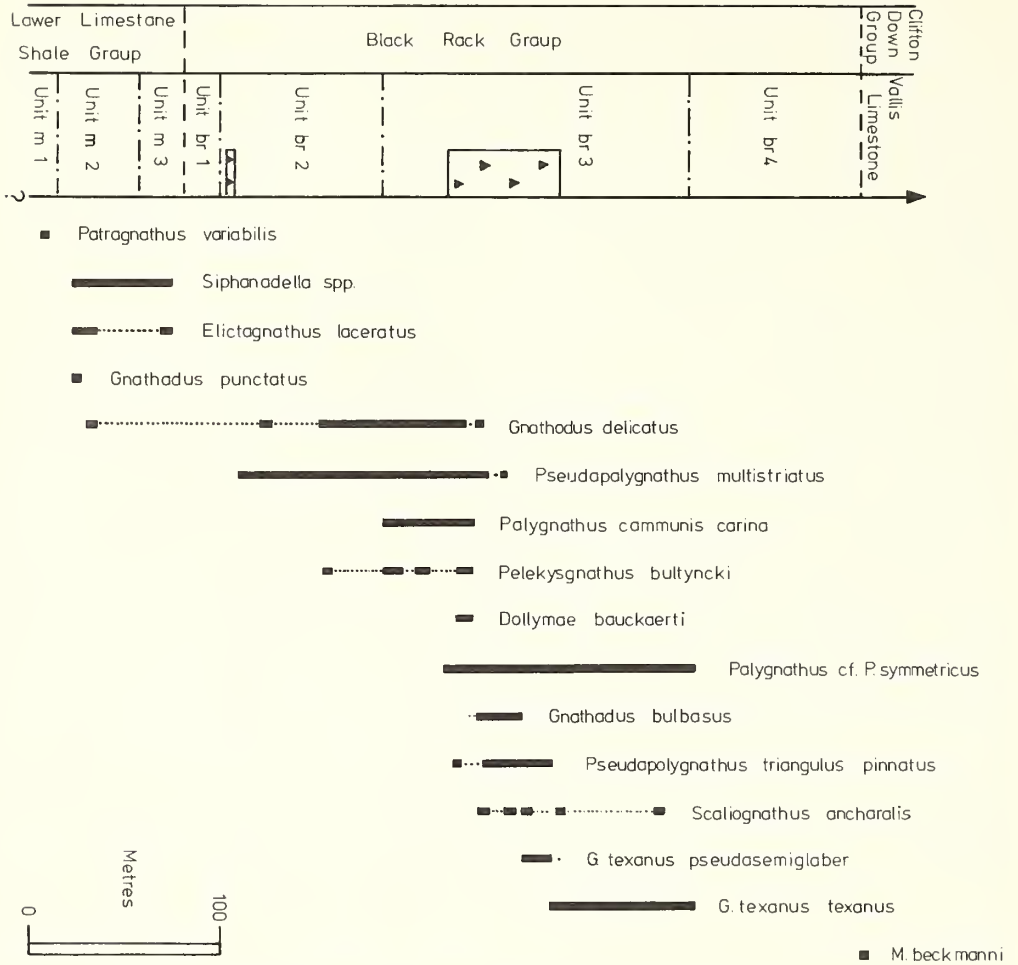
Samples were digested in 10% acetic acid and residues collected by sieving to 125-mesh sieve. Heavy liquid separation was carried out on the dried residues, using the methods described by Collinson (1963).

CONODONT OCCURRENCES IN THE EASTERN MENDIPS

Details of the occurrences of conodonts discussed here are available in text-figs. 3-10.

The Lower Limestone Shale Group. Conodont faunas recovered from the lowest part of the Lower Limestone Shale Group at Maesbury include *Polygnathus symmetricus* Branson and *Pseudopolygnathus dentilineatus* Branson. In addition, two specimens of *Patrognathus variabilis* Rhodes, Austin, and Druce were recovered from sample Ma 4.

At the base of unit m 2 coarse limestones with phosphatic nodules occur, forming a lag-type deposit, and an abrupt change in fauna takes place. The genera *Siphonodella*, *Elictognathus*, and *Gnathodus* first appear here (in sample Ma 7). The interval Ma 7 to Ma 19a is characterized by the presence of *Siphonodella obsoleta* Hass, *S. isosticha* (Cooper), *S. cf. S. isosticha* (Cooper), *S. cooperi* Hass, and *S. cf. crenulata* (Cooper). Two specimens of *Gnathodus punctatus* (Cooper) were recovered from sample Ma 7 and two specimens of *G. delicatus* Branson and Mehl were found in sample Ma 9. *Polygnathus inornatus* Branson ranges from Ma 7 to Ma 19a, and



TEXT-FIG. 2. Chart to show the ranges of selected conodont species in the Carboniferous Limestone of the eastern Mendips. See text-figs. 3 to 10 for full information. Firm lines represent proven ranges, broken lines are extrapolations.

Elictagnathus laceratus (Branson and Mehl) ranges from Ma 7 to Ma 19 but appears in only three samples.

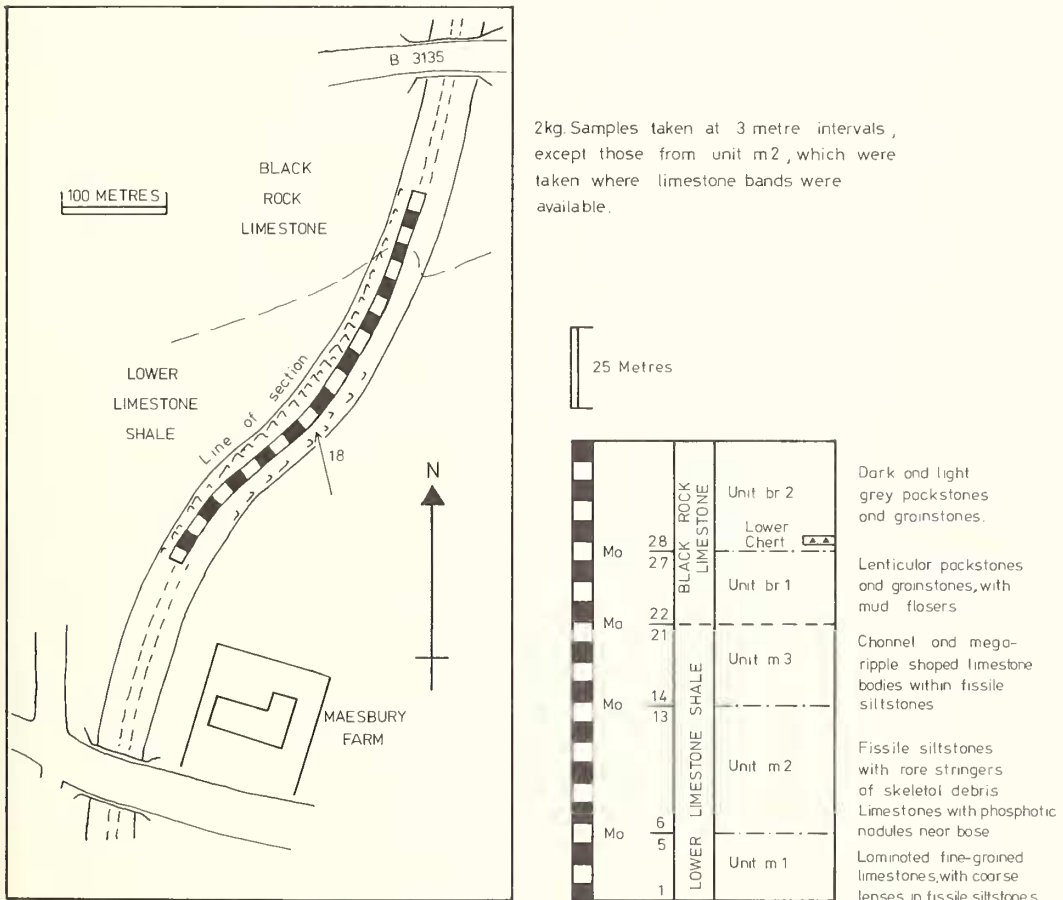
Sample Ma 20 marks another abrupt change in the conodont faunas, siphonodellids and associated forms disappearing. The fauna in this uppermost part of the Lower Limestone Shale Group includes *Polygnathus communis communis* Branson and Mehl and *Spathognathodus stabilis* (Branson and Mehl), and also includes poorly preserved specimens of *Spathognathodus aculeatus* (Branson and Mehl).

The Black Rock Group. The faunal assemblage seen in the uppermost part of the Lower Limestone Shale Group continues into the Black Rock Group. However, *Pseudopolygnathus multistriatus* Mehl and Thomas appears in sample WH 5, immediately above a minor chert development at the base of unit br 2, and *Sp. aculeatus*

is no longer seen. *Gnathodus delicatus* Branson and Mehl occurs in sample WH 12, but is not seen again until sample HW 2, where it becomes abundant. *Pseudopolygnathus primus* Branson and Mehl occurs in unit br 2. *Pelekysgnathus bultyncki* (Groessens) first appears in sample HW 3 and occurs along with *Polygnathus communis carina* Hass in samples HW 8 and HQ 1.

In the lower part of the Main Chert (unit br 3) at Ham Woods Quarry (samples HW 18 and HW 18a) there is an occurrence of abundant representatives of *Dollymaea bouckaerti* Groessens. This genus was not recovered from any other section. Associated with *D. bouckaerti* in these samples are *Pe. bultyncki*, *Ps. multistriatus*, and *Gnathodus delicatus*. In addition, a single specimen referable to *Doliognathus* sp. was recovered from HW 18.

Near the upper limit of the range of *P. communis carina*, *Gnathodus bulbosus* Thompson first appears (samples HW 20, HQ 12, and Va 2). *G. bulbosus* rapidly takes over from *G. delicatus* as the dominant gnathodid. At this level in both Ham Woods and Halecombe Quarries specimens referred to *Bactrognathus* cf. *B.*



TEXT-FIG. 3. Location of sampled section in Maesbury railway cutting (ST 606 475) and notes on lithologies.

MAESBURY	Samples	Ma	1	1a	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28		
Pseudopolygnathus dentilineatus			1	6																													
Polygnathus symmetricus			3	15	4	25	21																										
Patrognathus variabilis						2																											
Spathognathodus crassidentatus						1	1																										
P. communis communis						4		2	2		11		1						2			19	1			1							
Elictoagnathus laceratus									2		3											5											
Siphonodella isosticha										7	5	1	1									4	3										
S. cf. S. isosticha										1								1				3											
S. absoleta									1			1						1	1			11											
Polygnathus inornatus									68	3	40	3	10					3	11			11	2										
Spathognathodus stabilis									2													5			4		1						
Gnathodus punctatus									2																								
G. delicatus												3																					
Siphonadella cf. crenulata														2																			
Spathognathodus aculeatus																			1				3										
Siphonadella cooperi																						2	1										
Polygnathus sp.																						1											
Gnathodus sp. indet.											2																						
Siphonadella sp. indet.										8	2	3	3	6				1	3			21	2										
Spathognathodus sp. indet.					1			2		3	3	2	1			2				1	6	2	1	1	1	8							
BARs			6	4	9	6	6	39	8	28	7	14	5			5	5				85	7		13	2	30		1	2	1			
TOTAL			-	4	27	8	42	28	8	134	13	98	18	36	6	-	-	13	23	-	1	173	18	4	18	3	40	-	1	2	1	-	

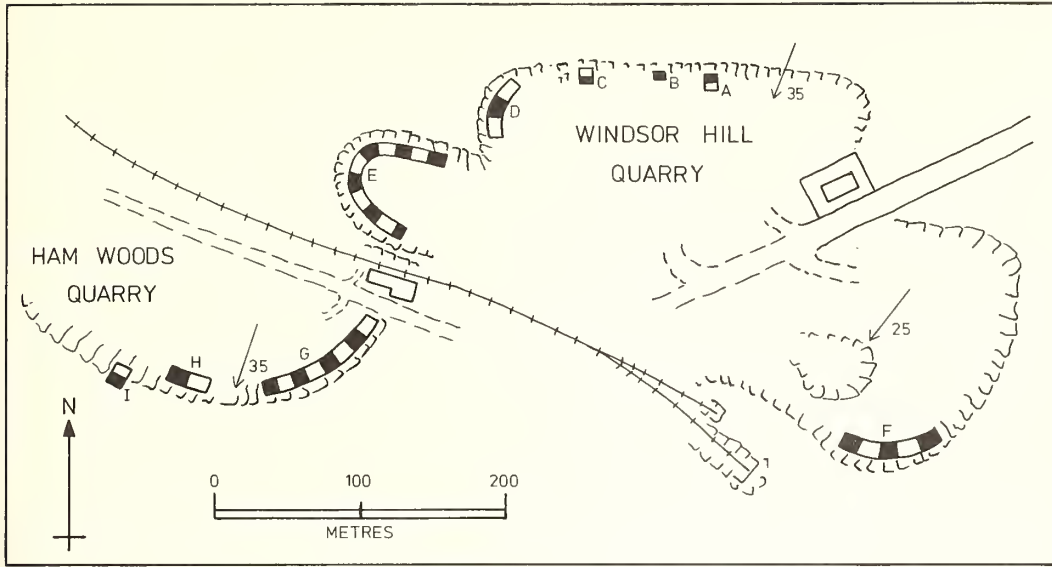
TEXT-FIG. 4. Chart to show conodont occurrences in samples from Maesbury railway cutting. (Sample prefix Ma.)

distortus Branson and Mehl occur (samples HW 21, 22, and HQ 14a). At Halecombe these are followed by the first occurrence of *Scaliognathus anchoralis* Branson and Mehl (in sample HQ 15). *Pseudopolygnathus triangulus pinnatus* Voges first appears in samples HW 23, HQ 16, and Va 1, and is an important constituent of the fauna in the middle part of unit br 3. *Pseudopolygnathus triangulus triangulus* Voges is present in samples throughout the range of *Ps. triangulus pinnatus*, although specimens possibly attributable to this subspecies also occur in samples HW 14 and HQ 14a.

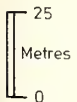
Ps. multistriatus dies out near the beginning of the range of *Ps. triangulus pinnatus* (sample HQ 19). Near the top of the range of *Ps. multistriatus*, *Polygnathus nodomarginatus* Branson makes a brief appearance. *Polygnathus* cf. *P. symmetricus* Branson first occurs here and ranges up into the top of unit br 3, where conodonts become rare.

In the middle part of unit br 3 both at Halecombe and in Vallis Vale (samples HQ 22 and Va 9) *G. bulbosus* disappears and *Gnathodus texanus pseudosemiglaber* Thompson and Fellows first appears. Towards the top of unit br 3 (samples HQ 32 and Va 13) *Gnathodus texanus texanus* Roundy first appears and *Ps. triangulus pinnatus* disappears. *Scaliognathus anchoralis* occurs in sample HQ 33, but is not seen again until HQ 46, where it is present together with *Hindeodella segaformis* Bischoff. A single specimen of *Pelekysgnathus* sp. A Voges was recovered from sample Va 13, and additional specimens of *H. segaformis* were also found in this sample.

Associated with *G. texanus texanus* and *P. cf. P. symmetricus* in the upper part of unit br 3 are common apatognathids and *Spathognathodus scitulus* (Hinde).



I	HW	23 22	BLACK ROCK LIMESTONE	Main Chert	▲ ▲ ▲	Dork grey, muddy crinoidal pockstones and wackestones	
H	HW	21 18 17					Unit br 3
G	HW	1					
F	WH	21 19 18		Unit br 2			Dork and light grey pockstones and grainstones. Cross-bedding occasionally visible
E	WH	10					
D	WH	9 7					
C	WH	6 5					
B	WH	4		Lower Chert	▲▲		Lenticular limestone bodies, with mud flasers.
A	WH	3 1					



2 kg. Samples taken at intervals of approximately 3 metres.

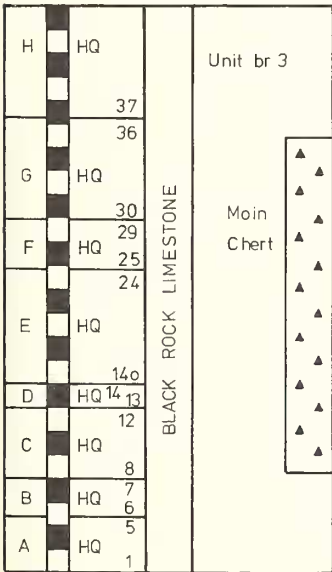
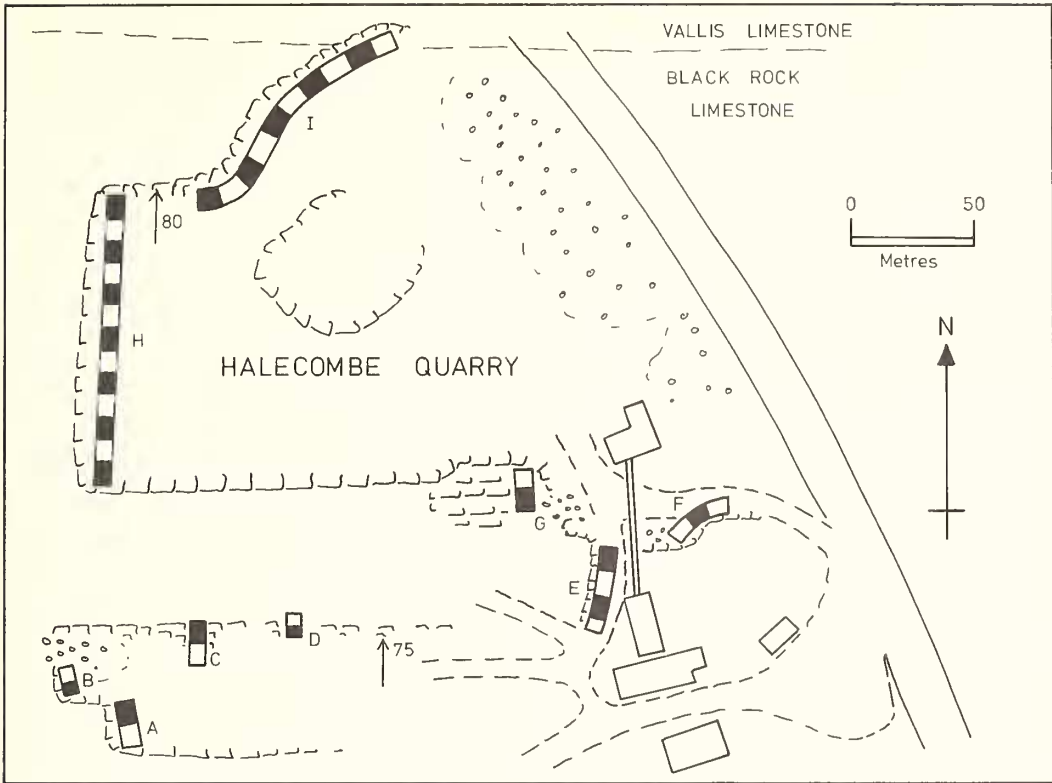
TEXT-FIG. 5. Location of sampled sections in Windsor Hill and Ham Woods Quarries (ST 615 452) and notes on lithologies.

WINDSOR HILL Qy. Samples WH	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
<i>Palygnathus communis communis</i>				1	5			2	1	6		7	1				2	3	4	2	
<i>Pseudapalygnathus multistriatus</i>					1			2	2	1	2	4				1	5	13	1	1	
<i>Spathagnathodus crassidentatus</i>					1			1											1	1	
<i>Sp. stabilis</i>												1					1	1			
<i>Ps. primus</i>												1					1	4			
<i>Gnathodus delicatus</i>												1									
<i>Spathagnathodus sp. indet.</i>		1				1	1	2	2		2							3	3		
BARS	3	5		3	25	1	5	4	4	10	1	24	3		1	11	17	20	7	3	2
TOTAL	3	6	-	4	32	2	5	10	9	19	3	40	4	-	1	12	26	44	16	6	3

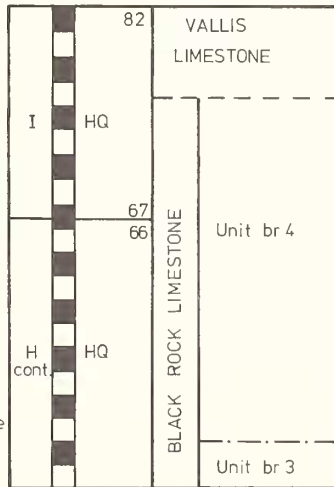
TEXT-FIG. 6. Chart to show conodont occurrences in samples from Windsor Hill Quarry. (Sample prefix WH.)

HAM WOODS Qy. Samples HW	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	18a	19	20	21	22	23
<i>Spathognathodus crossidentatus</i>	1	2				1	3	6		1						1								2
<i>Sp. stabilis</i>	2	2			1	1	3									2	18	5	1	10				
<i>Pseudopolygnathus multistriatus</i>	4	3			6	2	2	1									5			8				
<i>Ps. pastinadosus</i>	1																							
<i>Gnathodus delicatus</i>	2				3				17		8	3	7	9	6	6	116	31	10		1			5
<i>Pelekysgnathus bultyncki</i>		1					2											12						
<i>Polygnathus communis communis</i>	10	6	1	1	20			2		8	1	3	4	4	20	45	9			1	4			
<i>P. communis corino</i>							1	2		5	6	8	11	12	7	68	1							
<i>Gnathodus cf. delicatus</i>								2			1	1	1											
<i>Ps. triangulus cf. triangulus</i>												1												
<i>Polygnathus cf. P. symmetricus</i>																	2				16	3		6
<i>Dolymoe bouckoerti</i>																		57	6					
<i>Doliognathus sp.</i>																		1						
<i>P. nodomarginatus</i>																			1					
<i>Gnathodus n.sp. B. THOMPSON 1967</i>																			1		2			2
<i>G. bulbasus</i>																					19	11	28	33
<i>Bactrognathus cf. B. distartus</i>																						1	1	
<i>Ps. triangulus triangulus</i>																								1
<i>Ps. triangulus pinnotus</i>																								23
<i>Dolymoe sp.</i>																					1			
<i>Gnathodus sp. indet.</i>												1					11				6	2	1	
<i>Pseudopolygnathus sp. indet.</i>								1								3								
<i>Spathognathodus sp. indet.</i>	3	4			6	9	2	4		3								32	12	5	19	1		
BARS	4	60	27	3	34	20	1	19		15	2	1	13	20	11	154	31	17	28	24	24	72		
TOTAL	5	84	43	1	4	71	-	38	4	57	1	40	16	27	38	43	51	519	97	33	104	51	55	145

TEXT-FIG. 7. Chart to show conodont occurrences in samples from Ham Woods Quarry. (Sample prefix HW.)



Dork grey, muddy wackestone with Zoophycos. Few microfossils.



Light grey pelletal grainstone, with micritic introclasts.

Light grey crinoid - foraminifer grainstone.

Dork grey crinoidol pockstone and wackestone.

2 kg. Samples taken at intervals of approximately 3 metres.

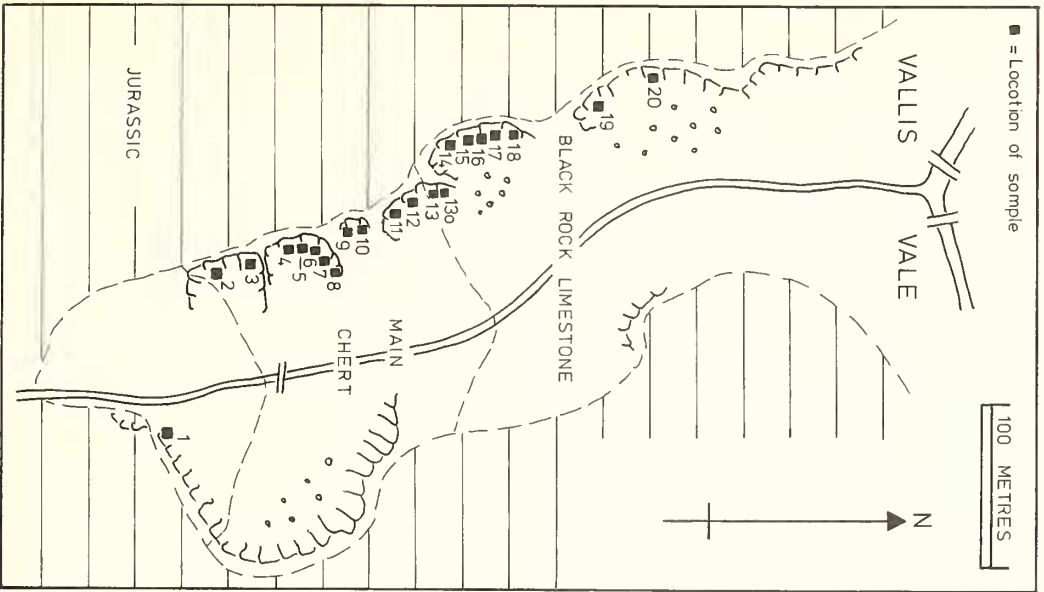
TEXT-FIG. 8. Location of sampled sections in Halecombe Quarry (ST 702 475) and notes on lithologies.

HALECOMBE Qy. Samples HQ	1	2	3	5	6	7	8	9	10	11	12	13	14	14a	15	16	17	18	19	20	21	22	23	24	25
<i>Pelekysgnathus butyncki</i>	2																								
<i>Pseudapalygnathus multistriatus</i>	2	1														1			1						
<i>Palygnathus communis communis</i>	6				6	4	3	2	9		11			4				1	34		1	86	34	3	6
<i>P. communis carina</i>	6					13	4	1	5																
<i>Gnathadus delicatus</i>	1	1	1			6	6	2	7			1													
<i>G. cf. delicatus</i>							1		1																
<i>Spathagnathadus stabilis</i>	1	3			1				2	1	7								1		1	11		1	2
<i>Sp. crassidentatus</i>		1							1	4								5				1			
<i>Palygnathus cf. P. symmetricus</i>								1		2	3			1	1		8	3	11		1	6	1		
<i>Gnathadus bulbosus</i>											1			18	124	11	26	55	25						
<i>Gnathadus n.sp. B, THOMPSON 1967</i>											1				1				2		1	5			
<i>Bactragnathus cf. B. distartus</i>														1											
<i>Ps. triangulus cf. triangulus</i>														1											
<i>Scaliagnathus ancharalis</i>																3		1				1			
<i>Ps. triangulus pinnatus</i>																	1	4	5				11	5	
<i>Palygnathus nadamarginatus</i>															1										
<i>Ps. triangulus triangulus</i>																		1							
<i>G. texanus pseudasemiglaber</i>																						5	1		
<i>Gnathadus sp. indet.</i>	1						1		1	5			10	17				3					1		
<i>Pseudapalygnathus sp. indet.</i>	1	1																	1	1		1			
<i>Spathagnathadus sp. indet.</i>			1		1			1	5	1	19											1	22		2
BARS	29	6	5	2	5	7	4	2	33	9	31		6	32	44	5	21	116	25	1	5	90	31	4	20
TOTAL	49	7	12	3	13	30	19	10	65	13	78	1	6	67	191	18	60	186	103	2	10	239	73	10	30

HALECOMBE Qy. Samples HQ	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	
<i>G. texanus pseudasemiglaber</i>	1		4	2																						
<i>Ps. triangulus pinnatus</i>			1			1																				
<i>Ps. triangulus triangulus</i>			3				1																			
<i>Spathagnathadus stabilis</i>	1	3				1				5	2	1		1			2	1	1							
<i>Sp. crassidentatus</i>		1								1				1												
<i>G. texanus texanus</i>							1			5		3				1			1		1		1		1	
<i>Palygnathus cf. P. symmetricus</i>			2	3			2	3		8	9		2	2	1		22	5		2	1		2		2	
<i>Scaliagnathus ancharalis</i>								1															1			
<i>Hindeadella segafarmis</i>																							1			
<i>Spathagnathadus scitulus</i>																	1					2	4			
apatagnathids																	5	1		1	2	5	1			
<i>Gnathadus sp. indet.</i>				2																						
<i>Spathagnathadus sp. indet.</i>						1	1				3			1			4									
BARS	2	7	36	24	3	17		4	3	30	6	8		14	2	2	77	8	1	3	17	6	3			
TOTAL	4	7	50	31	4	19	5	8	3	49	20	12	2	19	3	3	109	15	3	6	25	15	7	-	-	

HALECOMBE Qy. Samples HQ	52	54	56	58	60	62	64	66	68	70	72	74	75	76	78	80	82	
<i>Mestagnathus beckmanni</i>														2				
<i>Spathagnathadus sp. indet.</i>									1									
BARS														1	3			
TOTAL	-	-	-	-	-	-	-	-	1	-	-	-	-	1	5	-	-	-

TEXT-FIG. 9. Chart to show conodont occurrences in samples from Halecombe Quarry. (Sample prefix HQ.)



VALLIS VALE	Samples Va	1	2	3	4	5	6	7	8	9	10	11	12	13	13a	14	15	16	17	18	19	20	
<i>Polygnathus communis communis</i>		7	6								6	10											
<i>P. communis carino</i>		12																					
<i>Gnathodus delicatus</i>		4	10																				
<i>G. cf. delicatus</i>		1											1										
<i>Spathognathodus stabilis</i>		2									1	2	16	28	1	2	1	2	2	2	8		
<i>Sp. crossidentatus</i>		3	2																				
<i>Rs. triangulus pinnatus</i>		1				3	1				1						6	2					
<i>Polygnathus nadomorginatus</i>		1																					
<i>Gnathodus bulbosus</i>		27	1		36	2																	
<i>Pseudopolygnathus multistriatus</i>					3																		
<i>Gnathodus n.sp. B. THOMPSON 1967</i>						1																	
<i>Bactragnathus sp.</i>						1																	
<i>Polygnathus cf. P. symmetricus</i>								1	1		1	1	19	1	7	11	8	14	25				
<i>Glexonus pseudosemiglobus</i>									8	3	2	9	26	1									
<i>G. texonus texanus</i>												2	2	3						9	2		
<i>Pelekygnathus sp. A. VOGES 1959</i>												1											
<i>Hindeodella segotarmis</i>												2											
<i>apoloagnathids</i>																	1	2	9	4			
<i>Spathognathodus scitulus</i>																		2	1	1			
<i>Gnathodus sp. indet.</i>		6			2	1																	
<i>Pseudopolygnathus sp. indet.</i>		3								3													
<i>Spathognathodus sp. indet.</i>										5	3	2	9	4							4	9	3
BARS		2	23	4		53	8	4	11	6	18	6	82	28	21	5	6	21	23	90			2
TOTAL		32	78	5	-	99	12	4	12	30	35	13	117	370	28	17	19	39	67	133	-	2	

2kg. Samples. No regular sampling interval.

TEXT-FIG. 10. Location of samples from Vallis Vale (ST 755 490) and chart of conodont occurrences. (Sample prefix Va.)

Faunas from unit br 4 are particularly poor, only three samples producing any conodonts at all, and samples were processed from 6-metre intervals after HQ 50 (see text-fig. 11). Sample HQ 76 (at the base of the Vallis Limestone) produced two specimens of *Mestognathus beckmanni* Bischoff.

COMPARISONS AND CORRELATIONS WITH NORTH AMERICA AND EUROPE

Conodonts recovered during the course of this study are all referable to the Lower Carboniferous (Dinantian). The first definitive studies of conodonts of this age were carried out in Germany by Bischoff (1957) and Voges (1959). These authors erected a series of conodont zones for this part of the Carboniferous. In recent years it has become clear that although the German sections offer good information on the lowest Carboniferous and also on the *anchoralis*-Zone and higher levels, there is a paucity of information on the intermediate parts of the succession. The reason for this is that the rocks which include the *Siphonodella crenulata*-Zone of Voges (1959), that is the Liegende Alaunschiefer, have not produced good conodont faunas.

In Belgium, conodonts from that part of the succession characterized by the genus *Siphonodella* are still little known, although here again both lower and higher levels are better documented (for example, Conil *et al.* 1964; Conil *et al.* 1969; Austin *et al.* 1970). Groessens (1971) has recently described faunas of *anchoralis*-Zone age from Belgium. These latter faunas compare closely with some recovered during the present study.

In North America Collinson *et al.* (1962) erected a series of conodont zones for the Mississippian, based on evidence from the upper Mississippi Valley. These zones have been recently revised by Collinson *et al.* (1971). Recent work by Thompson (1967) and Thompson and Fellows (1970) has indicated that the upper Mississippi Valley sections are incomplete (see Collinson *et al.* 1971, fig. 2). It is with their more complete sequence of Mississippian rocks from south-western Missouri and Arkansas that the Mendip faunas best compare.

Lowest part of the Lower Limestone Shale Group at Maesbury. The conodonts from this part of the succession do not readily provide for detailed comparison with information from either German or North American sections. Voges (1959) found that *Pseudopolygnathus dentilineatus* has a range from the uppermost Devonian to the base of the *Siphonodella crenulata*-Zone, and possibly into that zone. This species has been reported from North America by several authors (for example Branson 1934; Collinson *et al.* 1962; Klapper 1966; Canis 1968) and has a range from basal Carboniferous, and possibly Upper Devonian, into the *Siphonodella quadruplicata*-*S. crenulata* Zone of Collinson *et al.* (1962). Thompson and Fellows (1970) reported *Ps. dentilineatus* ranging up into their *Gnathodus delicatus*-*Siphonodella cooperi cooperi* Zone. The genus *Patrognathus* has been recorded from the lowest Carboniferous of Belgium by Austin *et al.* (1970), but from an upper part of the Kinderhookian of North America by Klapper (1971). Klapper (1971) recovered the genus from within a range of stratigraphy which also yielded *Siphonodella isosticha* and *S. cooperi*, although siphonodellids and patrognathids were found together in only one sample.

It seems clear that the conodonts recovered from this part of the stratigraphy at Maesbury do not, at present, offer any possibility of precise correlation with other areas.

Faunas with Siphonodella. Siphonodellids first appear at Maesbury in beds which include phosphatic nodules and which are interpreted as lag concentrates. The species of *Siphonodella* present are advanced, in terms of the North American progression of forms (see Collinson *et al.* 1971), and their association with *Gnathodus punctatus* enables comparison to be made with what Thompson and Fellows (1970) regard as the uppermost Kinderhookian faunas. However, the ranges of *Gnathodus punctatus*, *G. delicatus*, *Siphonodella isosticha*, *S. obsoleta*, and *Elictognathus laceratus* are not shown to coincide on table 1 of Thompson and Fellows (1970). Their zonal scheme is not consistent with their own recorded results. An examination of the stratigraphic logs and conodont occurrence charts of these authors reveals that in the Baird Mountain Quarry section (Thompson and Fellows 1970, p. 149) several samples included this association of forms. Their samples 6 to 8 included *Gnathodus punctatus*, *G. delicatus*, *Siphonodella cooperi hassi* (= *S. isosticha*, *vide* Klapper, see systematic part), and *Elictognathus laceratus*, even though these forms do not have corresponding ranges in their table 1. Since these Baird Mountain Quarry samples are placed within the *Siphonodella cooperi hassi*-*Gnathodus punctatus* Zone, it would seem reasonable to correlate samples Ma 7 to Ma 19 with a part of this zone.

This zone of Thompson and Fellows (1970) represents a part of the stratigraphy which is not seen in the upper Mississippi Valley (Collinson *et al.* 1971, fig. 2). The uppermost Kinderhookian of the upper Mississippi Valley was correlated with the Belgian Tn 2b by Sando *et al.* (1969) on the basis of foraminiferids. Groessens (1971) gives an upper limit to the range of *Siphonodella* at the top of Tn 2c in Belgium. In Germany the range of the genus extends into the *anchoralis*-Zone (Voges 1959; Meischner 1971), and a similar situation has been noted in south-west England by Matthews (1969*a, b*). Matthews *et al.* (1972) report the occurrence of siphonodellids in a fauna including *Gnathodus punctatus*, *Dollymae hassi*, and *Polygnathus communis carina* from Devon.

A tentative correlation is here suggested between samples Ma 7 to Ma 19 and some part of the interval Tn 2b to Tn 2c in Belgium.

Uppermost Lower Limestone Shale Group and the lower part of the Black Rock Group. The lowest part of this interval is characterized by the dominance of *Pseudopolygnathus multistriatus* and *Polygnathus communis communis*. This association of forms conforms to faunas lying immediately above the range of *Siphonodella* in North America (for example Rexroad and Scott 1964) with the exception that there they include abundant gnathodids. There appears to be a scarcity of gnathodids throughout the Mendip sections at this time, these forms appearing in only two samples at Maesbury. Two possibilities emerge here: first, the lack of gnathodids at this level in the eastern Mendips could be due to some facies control; or secondly, this association of forms could be present in North America also, but has not been recognized since the successions there are thinner at this level. Further study of this problem is necessary. Whatever the cause of this absence, gnathodids reappear in the middle part of the Black Rock Group.

The first occurrence of *Polygnathus communis carina* is taken by Thompson and Fellows (1970) to define the lower limit of their *Gnathodus semiglaber*-*P. communis carina* Zone. This form first appears in sample HW 8 and is present in sample HQ 1. The first appearance of *Pseudopolygnathus multistriatus* is taken by Thompson and Fellows (1970) to mark the base of the overlying *Bactrognathus*-*Ps. multistriatus* Zone. This form appears earlier than *P. communis carina* in the Mendip successions (in sample WH 5). There does not appear to be any distinction to be made in the Mendip succession of conodonts between assemblages characteristic of the *Gnathodus semiglaber*-*P. communis carina* Zone and those of the *Bactrognathus*-*Ps. multistriatus* Zone of Thompson and Fellows (1970). Nor is it clear where the equivalent of the boundary between the *G. semiglaber*-*P. communis carina* Zone and the underlying *G. punctatus*-*Siphonodella cooperi hassi* Zone should be taken in the Mendips.

Pelekysgnathus bultyncki (Groessens) first appears in sample HW 3, but is present with *P. communis carina* in samples HW 8 and HQ 1. Groessens (1971) shows two maxima in the occurrence of *P. communis carina*, one of which coincides with the first appearance of *Pe. bultyncki*. It would seem reasonable to correlate sample HW 8 with a point near the beginning of the second maximum of *P. communis carina*, that is with the base of Tn 3c of Groessens (1971). In Belgium Groessens has shown that a level characterized by abundant *Dollymae bouckaerti* lies at the top of the range of *Pe. bultyncki*. Above this level *Doliognathus latus* makes a brief appearance and the range of *Scaliognathus anchoralis* begins. This progression of forms compares with that recognized in the Mendip successions. It is possible therefore to correlate with a fair degree of certainty between the eastern Mendips and Groessens's Belgian successions at these levels.

Fauyas comparable with the German anchoralis-Zone. The *anchoralis*-Zone was established in Germany by Bischoff (1957). Voges (1959, 1960) revised the zone and selected *Scaliognathus anchoralis*, *Hindeodella segaformis*, and *Doliognathus latus* as indices. Although *Scaliognathus anchoralis* was first described from North America by Branson and Mehl (1941), the *anchoralis*-Zone has not been widely recognized there. It is now clear that discontinuities within the Upper Mississippi Valley sections are in part responsible for this.

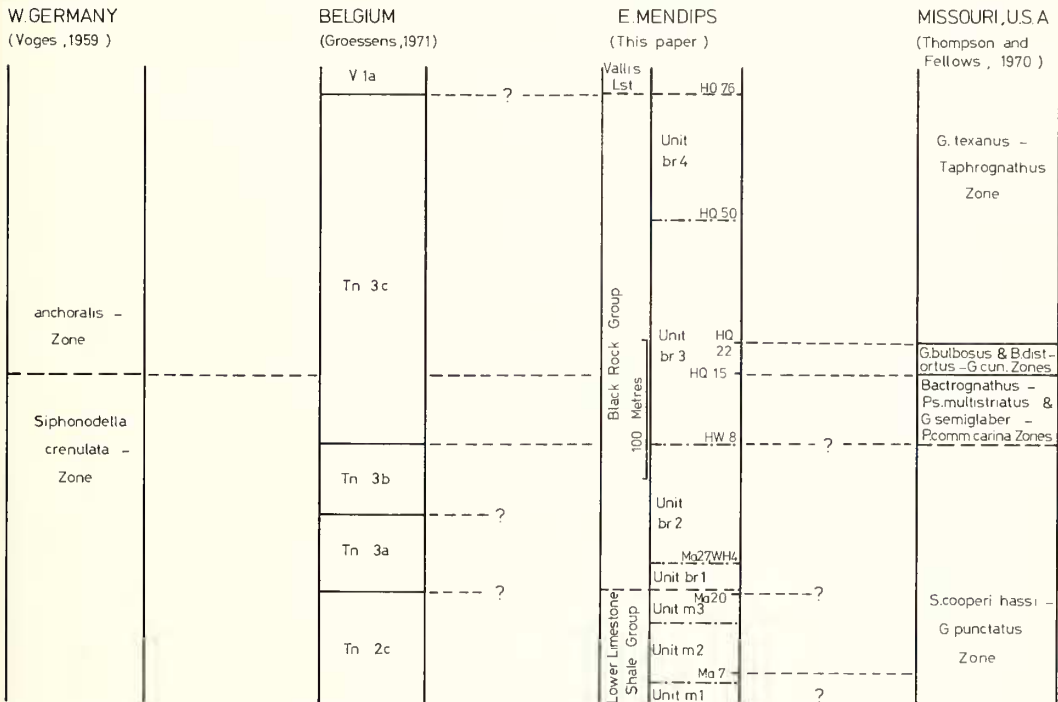
The recognition of a line of development leading to *Scaliognathus anchoralis* suggests that the first occurrence of this form at Halecombe Quarry must be at least as early as any occurrence elsewhere. Correlation is possible with Groessens's (1971) sections and with the base of the *anchoralis*-Zone in Germany.

Again it is necessary to point out some differences in the record of conodont occurrences between the eastern Mendip sections and those of Thompson and Fellows (1970). According to these authors the ranges of *Scaliognathus anchoralis* and *Pseudopolygnathus triangulus pinnatus* do not coincide with that of *Gnathodus bulbosus*. In the eastern Mendips, *Ps. triangulus pinnatus* and/or *Scaliognathus anchoralis* occur together with *G. bulbosus* in certain samples between HQ 15 and HQ 21 and with *G. texanus* subsp. in certain samples within the range HQ 22 to HQ 46. For the reasons given above, it seems unlikely that *Scaliognathus* would appear earlier in Thompson and Fellows's sections than it does in the eastern Mendips. The two first occurrences are therefore tentatively correlated, suggesting an equivalence

between sample HQ 15 and the base of the *Bactrognathus distortus*-*Gnathodus cuneiformis* Zone of Thompson and Fellows (1970).

The sequence of development from *G. bulbosus* to *G. texanus pseudosemiglaber* and *G. texanus texanus*, recognized by Thompson and Fellows (1970, p. 89) can also be seen in the Mendip faunas. The recognition of this sequence enables correlation to be made between sample HQ 22 and the base of the *Gnathodus texanus*-*Taphrognathus* Zone of Thompson and Fellows (1970), although it should be noted that no *Taphrognathus* has been recovered from the eastern Mendips. Below this zone in Thompson and Fellows's scheme lies the *Gnathodus bulbosus* Zone, which must fall within the interval HQ 15 to HQ 22 along with the *B. distortus*-*G. cuneiformis* Zone. As already stated, there seems to be no real distinction in the Mendips between the *G. semiglaber*-*P. communis carina* Zone and the *Bactrognathus*-*Ps. multistriatus* Zone. In addition it does not seem to be possible to separate a *B. distortus*-*G. cuneiformis* Zone from a *G. bulbosus* Zone here. It appears therefore that the four zones suggested by Thompson and Fellows (1970) for this part of the stratigraphy in Missouri and Arkansas resolve themselves into only two distinct divisions in the Mendips.

Groessens (1971) reported *Mestognathus beckmanni* from the uppermost part of Tn 3c and ranging up into the Viséan. Two specimens of *M. beckmanni* were recovered during the present study from a single sample (HQ 76) near the base of the Vallis Limestone. Voges (1959) reported *M. beckmanni* from the *anchoralis*-Zone,



TEXT-FIG. 11. Chart showing suggested correlations between the eastern Mendip composite section and sections in Europe and North America. Eastern Mendip column is drawn to scale, the others are not.

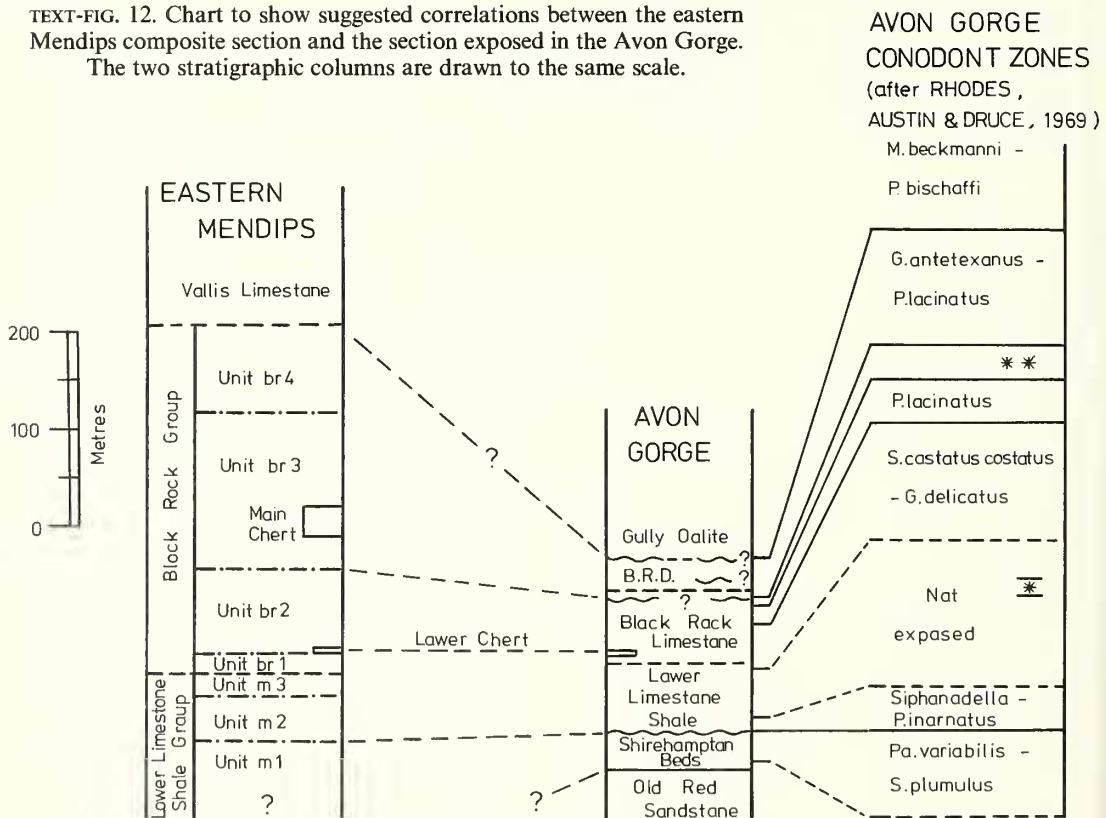
and it is therefore not possible to recognize an equivalent of zones higher than this in the sections studied.

Text-fig. 11 sets out the suggestions made here on correlation with sections in Europe and North America.

COMPARISONS AND CORRELATIONS WITH THE AVON GORGE

Rhodes *et al.* (1969) sampled the Lower Carboniferous succession in the Avon Gorge and compared it with a composite section from the North Crop of the South Wales Coalfield and with scattered sections in northern England and Scotland. They erected a zonal scheme, and suggested that facies-control might explain the absence of certain forms used as zonal indices in Germany and North America. This work has been criticized by Ziegler (1971) on methodological and other grounds. Among other points, Ziegler observes that it is difficult to extract from Rhodes *et al.* (1969) information on the exact occurrences and ranges of species and on the composition of faunas. This being the case, it will be understood that proposals on correlation between the Mendips and the Avon Gorge must be tentative at the present time. The proposals made here are set out in text-fig. 12, and discussed below.

TEXT-FIG. 12. Chart to show suggested correlations between the eastern Mendips composite section and the section exposed in the Avon Gorge. The two stratigraphic columns are drawn to the same scale.



* = *S. cf. S. rabustus* - *S. tridentatus* Zane (one isolated sample).
 ** = *P. lacinatus* - *Ps. cf. Ps. tangipasticus* Zane. B.R.D. = Black Rack Dalamite.

Faunas from the lowest parts of the Lower Limestone Shale Group (Samples K 1 to K 11 of Rhodes *et al.*; samples Ma 1 to Ma 6 of this paper). Faunas recovered from this part of the succession by Rhodes *et al.* (1969) include *Patrognathus*, *Pseudopolygnathus vogesi* (= *Ps. dentilineatus*, see systematic part), and also *Clydagnathus* and clydagnathid-like spathognathodids. This association compares in some respects with the Maesbury faunas, where *Patrognathus* was recovered from one sample and *Ps. dentilineatus* occurs in several samples.

It is possible that the absence of the clydagnathid group of conodonts at Maesbury may be explained by restriction of these conodonts to a narrow range of facies. They occur both at Portishead and Clevedon (see Appendix) in facies different from that of the Shirehampton Beds in the Avon Gorge, but it may be worth while to note that in the North Crop, where stromatolitic and oolitic rocks predominate (George 1954), this group of conodonts extends into the Z zone (Black Rock Group) (Rhodes *et al.* 1969).

The Palate Bed in the Avon Gorge (which lies between samples K 11 and K 12 of Rhodes *et al.* 1969) contains a large conodont fauna, including abraded specimens (see Appendix). *Siphonodella duplicata* appears in this bed, but has not been reported from elsewhere in the Bristol district. A discontinuity is present below the Palate Bed in the Avon Gorge. Caliche formation occurred within the underlying Bryozoa Bed, and pebbles of Bryozoa Bed material occur within the Palate Bed. The possibility cannot therefore be ruled out that the lower part of the Maesbury section (unit m 1) might include faunas which have no representation in the discontinuous Avon Gorge stratigraphy.

Faunas with *Siphonodella* (Samples K 12 and K 17 of Rhodes *et al.*; Samples Ma 7 to Ma 19a of this paper). Rhodes *et al.* (1969) recovered two specimens of *Siphonodella* from the Avon Gorge. Both were broken, but were identified as advanced forms on the basis of the rostral ridge development (Rhodes *et al.* 1969, p. 55). Patrognathids occur with these siphonodellids in the Avon Gorge. Both at Maesbury and in the Avon Gorge the incoming of siphonodellids is associated with a phosphatic lag deposit. At this level a comparison is therefore possible both in faunal and sedimentological terms.

The presence of patrognathids along with the siphonodellids in the Avon Gorge section could be due entirely to reworking associated with the Palate Bed, which (see Appendix) certainly includes reworked patrognathids. It is also possible that facies differences play some part in this. This problem may become clearer when the full distribution of *Patrognathus* is known.

It should be noted that in a later paper, Austin *et al.* (1971, text-fig. 2) extend the range of *Siphonodella* below the Bryozoa Bed. There is no justification for this on the basis of any published information. In the Avon Gorge a covered interval is present above sample K 17 of Rhodes *et al.* (1969). In their paper these authors give this interval as 25 ft (7.5 m) (Rhodes *et al.* 1969, fig. 59). This gap has been recognized by other workers and is usually given a value of some 200 ft (60 m). Thus, Kellaway (1971) gives the total thickness of the Lower Limestone Shale Group in the Avon Gorge as 350 ft (107 m) compared with the 175 ft (53.5 m) given by Rhodes *et al.* (1969). This covered interval may, in part, explain the rarity of siphonodellids in the Avon Gorge reported by Rhodes *et al.* (1969).

Faunas from the uppermost part of the Lower Limestone Shale Group and those from the lower part of the Black Rock Group (Samples K₂ 1 to Z 37 of Rhodes *et al.*; Samples Ma 20 to Ma 28; WH 1 to WH 21; HW 1 to HW 22; HQ 1 to HQ 14a; Va 1 to Va 2 of this paper). Faunas recovered from this part of the succession by Rhodes *et al.* (1969) compare well with those from the Mendips. In the lower part of this interval the faunas are dominated by *Pseudopolygnathus multistriatus* (see systematic description for synonymy) and *Polygnathus communis communis*. *Gnathodus delicatus* appears some way above the base of the Black Rock Limestone (Z zone). It should be noted here that Rhodes *et al.* (1969) did not in fact recover *Gnathodus delicatus* from their *Spathognathodus costatus costatus*-*Gnathodus delicatus* Zone in the Avon Gorge. The first occurrence of *G. delicatus* there is given by Rhodes *et al.* (1969, p. 97) as sample Z 28, and this may tentatively be correlated with the point where gnathodids become abundant in the Mendips, that is sample HW 2 at Ham Woods Quarry.

The lower chert horizon noted in the Mendips is represented in the Avon Gorge (sample Z 13 of Rhodes *et al.* 1969, fig. 60). However, the Main Chert is not present there, nor are any of the conodonts found at this level in the Mendip succession. *Polygnathus communis carina* was not reported from the Avon Gorge and no conodonts of the kind of *Pelekysgnathus bultyncki* or *Dollymae bouckaerti* were recorded. Since *P. communis carina* first appears in sample HW 8 in the Mendips, it seems likely that the interval Z 28 (the first appearance of *G. delicatus*) to Z 37 (first appearance of *G. bulbosus* in Z 38, see below) in the Avon Gorge lies below the level of HW 8 in the Mendips, but above that of HW 2.

An equivalence appears therefore to have been established between the uppermost part of the Black Rock Limestone (Z zone) in the Avon Gorge and a level less than half-way up this division in the Mendips. It seems that a considerable discontinuity may exist at the top of the Black Rock Limestone in the Avon Gorge, as has already been suggested by Mitchell (1971, 1972) on the basis of coral faunas.

Faunas comparable with the German anchoralis-Zone (Samples Z 38 to C 14 of Rhodes *et al.*; Samples HW 23; HQ 15 to HQ 82; Va 3 to Va 20 of this paper). Rhodes *et al.* (1969) did not record any trace of anchoralis-Zone faunas (with the exception of one specimen of *Pseudopolygnathus triangulus* cf. *pinnatus*, which is removed from this species altogether in the systematic part of this paper, see below). However, an examination of their faunas from the Black Rock Dolomite in the Avon Gorge has revealed that certain gnathodids characteristic of the anchoralis-Zone equivalents in the Mendips do in fact occur here. Thus, *G. bulbosus* occurs in sample Z 38 and *G. texanus pseudosemiglaber* occurs in sample C 4. S. C. Matthews (pers. comm.) has recovered *Ps. triangulus pinnatus* from the Black Rock Dolomite in the Avon Gorge.

It appears therefore that although the Mendip succession is much the thicker at this level, and the Avon Gorge succession broken, there might nevertheless be some isolated remnants of the fuller succession of faunas to be found in the Black Rock Dolomite at Bristol. All of this question will be clearer when the conodont faunas of the Black Rock Dolomite have been restudied.

Sparse faunas with *Mestognathus beckmanni* were recorded from the Gully Oolite of the Clifton Down Group in the Avon Gorge by Rhodes *et al.* (1969), and

they may perhaps be compared with those recovered from sample HQ 76 in the Mendips. This would indicate that the base of the Gully Oolite in the Avon Gorge is no lower than the top of the Black Rock Group in the eastern Mendips, which is consistent with the proposals advanced by Kellaway and Welch (1955). Mitchell (1972) has recently suggested that the Tournaisian-Viséan boundary should lie at, or below, the base of the Gully Oolite in the Avon Gorge. The conodont faunas recovered from the eastern Mendips during this study do not contradict this suggestion when compared with those recovered from Belgium by Groessens (1971).

SYSTEMATIC PALAEOLOGY

The entire conodont collection has been deposited in the Leeds Office of the Institute of Geological Sciences. Four-figure numbers prefixed LZA identity 32-cavity slides in the collection. Individual cavities are identified by a suffix to the four-figure number. Each figured specimen occupies its own cavity. Bar-type conodonts are included in the collection, but since they have in almost every case no stratigraphic significance, they are not treated in the systematics. The sole exception is *Hindeodella segaformis*.

The synonymy lists carry annotations according to the system proposed by Richter (1948).

Genus BACTROGNATHUS Branson and Mehl 1941

Bactrognathus cf. *B. distortus* Branson and Mehl 1941

Plate 58, figs. 11-13

Remarks. This form possesses a posterior lateral process, suggesting comparison with the genus *Bactrognathus*. The prominent hornlike denticle is similar to that described for *B. distortus* Branson and Mehl by Rexroad and Scott (1964). These authors figure a lateral view of *B. distortus* which is similar to that of the present specimens (cf. Rexroad and Scott 1964, pl. 3, fig. 9). The distal part of the posterior lateral process of *B. distortus* is, however, normally redirected towards the posterior, giving a Z-shaped appearance in oral view.

In lateral view the main bar resembles that of *Pelekysgnathus bultyncki* (Groessens) and in oral view the species has much in common with immature forms of *Scaliognathus anchoralis* Branson and Mehl, which, however, have two posterior lateral processes (cf. Pl. 58, figs. 12, 13, and figs. 21, 22).

Material. 3 specimens, from 3 samples.

Genus DOLIOGNATHUS Branson and Mehl 1941

Doliognathus sp.

Plate 58, figs. 17, 18

Remarks. A single specimen referable to this genus was recovered in association with *Pelekysgnathus bultyncki* (Groessens) and *D. bouckaerti* Groessens. It resembles early forms of *Pe. bultyncki*, displaying a short posterior bar behind the prominent hornlike denticle, but has a small node on the inner side of this denticle.

The basal cavity has a corresponding lobe underneath this lateral node. Although this specimen is an immature form, it is considered to resemble the genus *Doliognathus* Branson and Mehl. The lateral view of a specimen assigned to *D. latus* Branson and Mehl by Groessens (1971, pl. 2, fig. 1) is similar in appearance.

Material. 1 specimen.

Genus DOLLYMAE Hass 1959
Dollymae bouckaerti Groessens 1971

Plate 58, figs. 19, 20, 25, 26

1959 *Dollymae* sp. B Voges, p. 276, pl. 33, figs. 15-17.

*1971 *Dollymae bouckaerti* Groessens, p. 14, pl. 1, figs. 6-8.

Remarks. Specimens found during the present study demonstrate similar morphological variations to those described by Groessens (1971). The diagnosis given by Groessens (1971, p. 14) runs as follows: 'A species of the genus *Dollymae* with a straight blade and two lateral processes, each ornamented by a single node or row of nodes. The basal cavity occupies the whole of the aboral surface of the platform and includes a median groove.'

In agreement with Groessens (1971, p. 15) this species is considered to have been derived from his own *Spathognathodus bultyncki* (referred to *Pelekysgnathus* below) by an expansion of the basal cavity and the development of nodes on the resulting lateral processes.

Material. 63 specimens, from 2 samples.

Dollymae sp.

Remarks. A single specimen referable to the genus *Dollymae* Hass was recovered from sample HW 20. This specimen was broken, only part of the platform and lateral process from one side being found. The specimen shows the development of a broad basal cavity, with a platform ornamented by a laterally directed arc-shaped row of denticles. The platform ornamentation does not fall within the range of variation of that of *D. bouckaerti* Groessens.

Material. 1 specimen.

Genus ELICTOGNATHUS Cooper 1939
Elictoognathus laceratus (Branson and Mehl 1934)

Plate 59, figs. 25, 28

*1934 *Solenognathus lacerata* Branson and Mehl, p. 271, pl. 22, figs. 5, 6.

1970 *Elictoognathus laceratus* (Branson and Mehl); Thompson and Fellows, p. 81, pl. 5, figs. 20, 21 (with synonymy).

Remarks. Klapper (1966) and Thompson and Fellows (1970) have discussed the range of variation in ornament exhibited by this species. Specimens recovered from Maesbury are simple forms, similar to Branson and Mehl's holotype.

Material. 10 specimens, from 3 samples.

Genus GNATHODUS Pander 1856

Remarks. In recent years much confusion has arisen in the classification of gnathodids, particularly in that of *G. texanus* Roundy. It is now becoming clear that part of the reason for this is that the record of gnathodids from the upper Mississippi Valley is not complete (compare Rexroad and Scott 1964 and Thompson and Fellows 1970). In addition, the stratigraphy immediately below the *anchoralis*-Zone in Germany has not produced many conodonts. It now appears that the gnathodids referred to as *G. antetexanus* Rexroad and Scott lie below the *anchoralis*-Zone and that the German *anchoralis*-Zone gnathodids (including the *G. texanus* group of Voges 1959) are not represented in the upper Mississippi Valley sections.

In the eastern Mendips, *G. delicatus* Branson and Mehl dominates faunas immediately below the *anchoralis*-Zone and faunas in the lower part of this zone are dominated by *G. bulbosus* Thompson.

Gnathodus bulbosus Thompson 1967

Plate 56, figs. 12, 15, 16, 19-24, 27

- *1967 *Gnathodus bulbosus* Thompson, p. 37, pl. 3, figs. 7, 11, 14, 15, 18-21; pl. 6, figs. 2, 7.
- v1969 *Gnathodus punctatus* (Cooper); Rhodes, Austin, and Druce, p. 105, pl. 18, figs. 1, 10, 11.
- v1969 *Gnathodus punctatus*-*Gnathodus semiglaber* transition; Rhodes, Austin, and Druce, pl. 30, figs. 2, 8.
- 1970 *Gnathodus bulbosus* Thompson; Thompson and Fellows, p. 84, pl. 1, figs. 3, 6, 8, 9, 12, 13.

Remarks. Thompson (1967, p. 37) restricted this species to those forms whose carina is bulbous where it protrudes beyond the posterior end of the platform. Specimens he illustrated are characterized by high peg-like nodes at the anterior end of the platform, appearing almost to 'pinch' the carina. In the present study, many specimens possess further nodes lying in rows parallel to the carina in the posterior part of the platform. These are considered to lie within the range of variation of *G. bulbosus*.

As suggested by Thompson and Fellows (1970, p. 89) *G. texanus* Roundy appears to have developed from *G. bulbosus* by a reduction of the platform and the expansion of the peg-like inner node into a short parapet.

Material. 417 specimens, from 15 samples.

Gnathodus delicatus Branson and Mehl 1938

Plate 56, figs. 3-5, 7-11, 13, 14

- *1938 *Gnathodus delicatus* Branson and Mehl, pl. 34, p. 145, figs. 25-37.
- 1967 *Gnathodus* sp. cf. *bilineatus* (Roundy); Thompson, p. 37, pl. 3, figs. 8, 10, 12, 17.
- v1969 *Gnathodus semiglaber* Bischoff; Rhodes, Austin, and Druce, p. 106, pl. 30, fig. 1.
- 1970 *Gnathodus* sp. cf. *bilineatus* (Roundy); Thompson and Fellows, p. 84, pl. 1, figs. 5, 10.
- v1972 *Gnathodus delicatus* Branson and Mehl; Matthews, Sadler, and Selwood, pp. 559-560, pl. 110, figs. 5, 7-9 (with synonymy).

Remarks. This species is considered to include all those gnathodids which possess platforms ornamented by rows of nodes sub-parallel to the carina, but without the low broad outer platform characteristic of *G. bilineatus* (Roundy). Forms towards

the top of the range of the species show the development of a distinct parapet, situated anteriorly on the inner side, the rows of nodes posterior to it being less well developed. These forms resemble those called *G. antetexanus* Rexroad and Scott and *G. typicus* Cooper but are here considered to lie within the range of variation of *G. delicatus*. A transition exists between *G. delicatus* and forms with a bulbous platform on the inner side, referable to *G. semiglaber* Bischoff. Matthews *et al.* (1972) have drawn attention to forms of *G. delicatus* which resemble *G. punctatus* (Cooper). The specimen illustrated here in Plate 56, figs. 10, 11 is of this type.

Material. 275 specimens, including 8 cf. determinations, from 27 samples.

Gnathodus punctatus (Cooper 1939)

Plate 56, figs. 1, 2

- *1939 *Dryphenotus punctatus* Cooper, p. 386, pl. 41, figs. 42, 43; pl. 42, figs. 10, 11.
 v1972 *Gnathodus punctatus* (Cooper); Matthews, Sadler, and Selwood, pp. 560-562, pl. 109, figs. 5, 13; pl. 110, figs. 1-4, 11-15 (with synonymy).

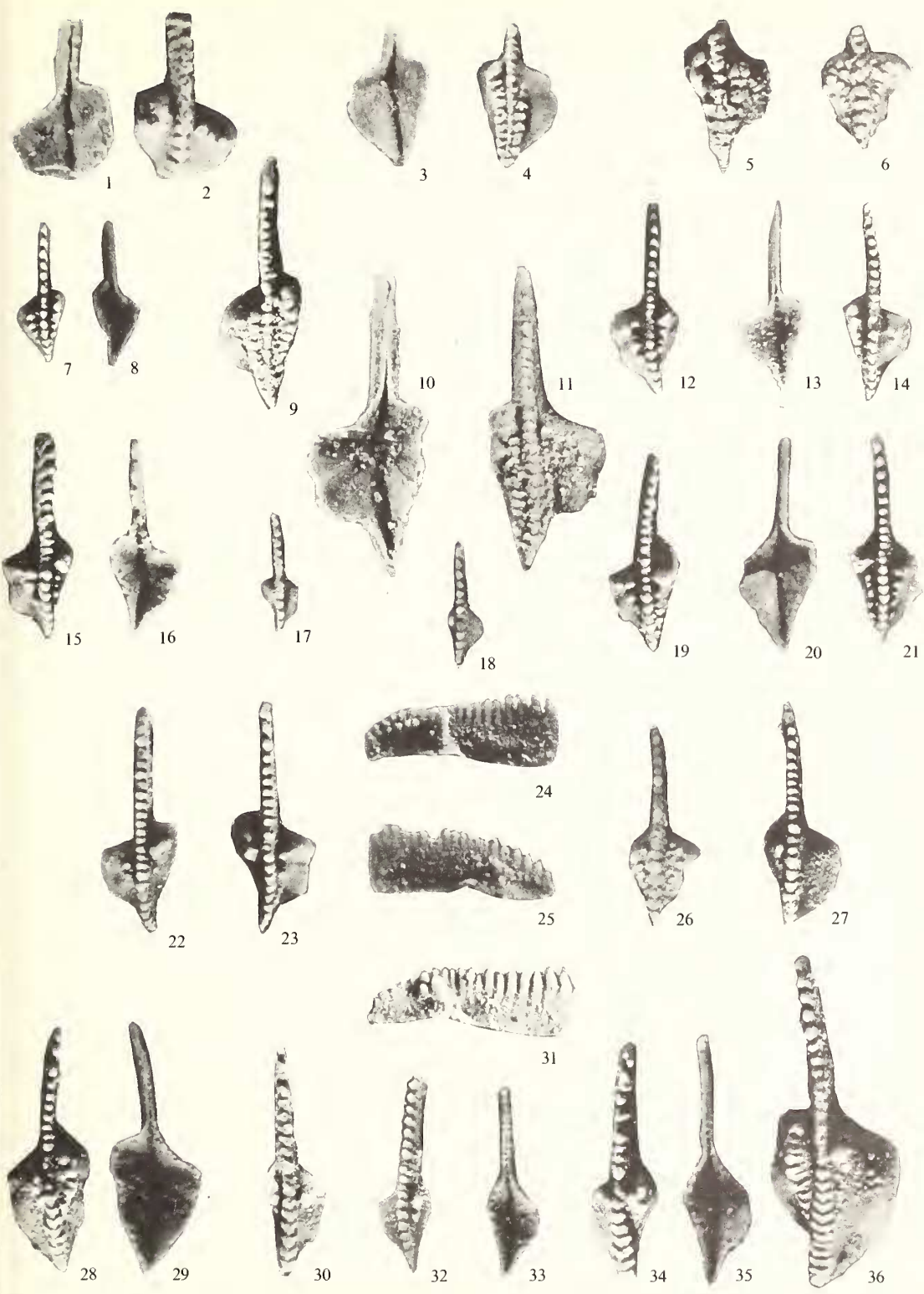
Remarks. Matthews *et al.* (1972) have described several variants of this species. The two specimens recovered during the present study both lie within variant 5 of these authors. A specimen illustrated by Rhodes *et al.* (1969) as *G. delicatus* is considered here to lie within the range of variation of *G. punctatus* (variant 1 of Matthews *et al.* 1972, and cf. Plate 56, figs. 10, 11 of this paper). Specimens referred to *G. punctatus* by Rhodes *et al.* (1969) are placed in *G. bulbosus* (see above). *G. punctatus* has a curved inner parapet, convex to the carina, and is therefore distinguished from *G. bulbosus*, which has a peg-like node on the inner side.

Material. 2 specimens, from 1 sample.

EXPLANATION OF PLATE 56

Specimens dusted with ammonium chloride. All $\times 30$.

- Figs. 1, 2. *Gnathodus punctatus* (Cooper). Aboral and oral views of LZA 6008/1 (sample Ma 7).
 Figs. 3-5, 7-11, 13, 14. *Gnathodus delicatus* Branson and Mehl. 3, 4, Aboral and oral views of LZA 6060/1 (HW 10). 5, LZA 6010/1 (Ma 9). 7, 8, Oral and aboral views of LZA 6086/1 (HQ 10). 9, LZA 6080/1 (HQ 3). 10, 11, Aboral and oral views of LZA 6063/1 (HW 13). 13, 14, Aboral and oral views of LZA 6068/10 (HW 18).
 Figs. 6, 25, 26. *Gnathodus* n. sp. B Thompson, 1967. 6, LZA 6077/4 (HW 23). 25, 26, Lateral and oral views of LZA 6093/4 (HQ 15).
 Figs. 12, 15, 16, 19-24, 27. *Gnathodus bulbosus* Thompson. 12, LZA 6093/6 (HQ 15): specimen transitional from *G. delicatus*. 15, 16, Oral and aboral views of LZA 6093/1 (HQ 15). 19, LZA 6093/9 (HQ 15). 20, 21, Aboral and oral views of LZA 6100/1 (HQ 19). 22, LZA 6093/2 (HQ 15). 23, LZA 6093/5 (HQ 15). 24, LZA 6093/3 (HQ 15). 27, LZA 6098/1 (HQ 18).
 Figs. 17, 18. *Gnathodus* sp. (juv?). 17, LZA 6093/7 (HQ 15). 18, LZA 6093/8 (HQ 15).
 Figs. 28, 29, 36. *Gnathodus texanus pseudosemiglaber* Thompson and Fellows. 28, 29, Oral and aboral views of LZA 6112/3 (HQ 29). 36, LZA 6150/1 (Va 13).
 Figs. 30-35. *Gnathodus texanus texanus* Roundy. 30, LZA 6118/5 (HQ 35). 31-33, Lateral, oral, and aboral views of LZA 6118/1 (HQ 35). 34, 35, Oral and aboral views of LZA 6155/1 (Va 17).



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Gnathodus texanus Roundy 1926

Remarks. Thompson and Fellows (1970) have recognized two subspecies of *G. texanus* Roundy. Both have been recovered from the eastern Mendips.

Gnathodus texanus pseudosemiglaber Thompson and Fellows 1970

Plate 56, figs. 28, 29, 36

- ?1967 *Gnathodus texanus* Roundy; Wirth, p. 213, pl. 23, fig. 18 (only).
 v. 1969 *Gnathodus antetexanus* Rexroad and Scott; Rhodes, Austin, and Druce, pl. 18, fig. 13 (only).
 *1970 *Gnathodus texanus pseudosemiglaber* Thompson and Fellows, p. 88, pl. 2, figs. 6, 8, 9, 11-13 (with synonymy).
 ?1970 *Gnathodus typicus* Cooper; Marks and Wensink, p. 264, pl. 4, figs. 1, 4 (only).

Remarks. Thompson and Fellows (1970, p. 89) suggest that this form arises from *G. bulbosus* and in turn gives rise to *G. texanus texanus* Roundy. This view is supported by evidence from the eastern Mendips. Specimens recovered are similar to those illustrated by Thompson and Fellows (1970).

Material. 62 specimens, from 11 samples.

Gnathodus texanus texanus Roundy 1926

Plate 56, figs. 30-35

- *1926 *Gnathodus texanus* Roundy, in Roundy, Girty, and Goldman, p. 12, pl. 2, figs. 7, 8.
 1970 *Gnathodus texanus texanus* Roundy; Thompson and Fellows, p. 89, pl. 2, figs. 15, 16 (with synonymy).
 ?1970 *Gnathodus typicus* Cooper; Marks and Wensink, p. 264, pl. 4, figs. 2, 3 (only).

Remarks. Specimens recovered from the eastern Mendips conform to the description given by Thompson and Fellows (1970, p. 89). As these authors suggest, the subspecies seems to develop from *G. texanus pseudosemiglaber* by a reduction of the outer platform.

Material. 31 specimens, from 12 samples.

Gnathodus n. sp. B Thompson 1967

Plate 56, figs. 6, 25, 26

- 1967 *Gnathodus* n. sp. B Thompson, p. 43, pl. 4, figs. 1-4.

Remarks. This species is characterized by a platform ornamented by scattered low nodes or rows of nodes. It may deserve to be included within the range of variation of *G. delicatus*.

Material. 16 specimens, from 9 samples.

Genus HINDEODELLA Ulrich and Bassler 1926

Hindeodella segaformis Bischoff 1957

Plate 58, fig. 29

- *1957 *Hindeodella segaformis* Bischoff, p. 28, pl. 5, figs. 40, 41, 43.
 1959 *Hindeodella segaformis* Bischoff; Voges, p. 285.

- 1964 *Hindeodella segaformis* Bischoff; Burton, range chart, facing p. 74.
 1965 *Hindeodella segaformis* Bischoff; Budinger, p. 66, pl. 5, figs. 19-21 (with synonymy).
 1967 *Hindeodella segaformis* Bischoff; Zikmundová, pl. 2, fig. 3; pl. 3, figs. 2a, 2b.
 1969a *Hindeodella segaformis* Bischoff; Matthews, pl. 47, figs. 10, 11.
 1970 *Hindeodella segaformis* Bischoff; Marks and Wensink, p. 265, pl. 1, fig. 2.

Material. 3 specimens, from 2 samples.

Genus MESTOGNATHUS Bischoff 1957
Mestognathus beckmanni Bischoff 1957

Plate 58, figs. 1, 2

- *1957 *Mestognathus beckmanni* Bischoff, p. 37, pl. 2, figs. 4, 5, 6, 8, 9.
 1960 *Mestognathus beckmanni* Bischoff; Ziegler in Kronberg, Pilger, Scherp, and Ziegler, p. 14, pl. 3, fig. 1.
 v1969 *Mestognathus beckmanni* Bischoff; Rhodes, Austin, and Druce, p. 150, pl. 15, fig. 7.
 1971 *Mestognathus beckmanni* Bischoff; Groessens, pl. 2, fig. 8.

Material. 2 specimens, from 1 sample.

Genus PATROGNATHUS Rhodes, Austin, and Druce 1969
Patrognathus variabilis Rhodes, Austin, and Druce 1969

Plate 59, figs. 1, 2

- v*1969 *Patrognathus variabilis* Rhodes, Austin, and Druce, p. 179, pl. 2, figs. 8-11.
 1970 *Patrognathus variabilis* Rhodes, Austin, and Druce; Austin, Conil, Rhodes, and Streel, pl. 1, fig. 7.

Remarks. Klapper (1971) has distinguished two species of *Patrognathus*, based on the size of the basal cavity. The two specimens recovered from the Maesbury section have widely-flared basal cavities and can therefore be included in *P. variabilis*.

Material. 2 specimens, from 1 sample.

Genus PELEKYSGNATHUS Thomas 1949

Remarks. This genus was originally described from Upper Devonian rocks. Voges (1959) reported its occurrence in rocks of *anchoralis*-Zone age, and further records from Carboniferous rocks of this age have come from New Mexico (Burton 1964) and Belgium (Groessens 1971). Klapper (1966) has discussed the difficulty of distinguishing *Pelekysgnathus* from *Icriodus* in the Upper Devonian. Forms recovered from the eastern Mendips are here referred to as *Pelekysgnathus*, following the lead of Voges (1959). The relationship of these to any Devonian forms, whether *Pelekysgnathus* or *Icriodus*, is not understood.

Pelekysgnathus bultyncki (Groessens 1971)

Plate 58, figs. 8-10, 14-16

- *1971 *Spathognathodus bultyncki* Groessens, p. 115, pl. 1, figs. 2-5.

Remarks. Groessens's diagnosis (1971, p. 15) runs as follows: 'A species of *Spathognathodus* with a straight, or slightly arched, blade. The denticles are upright in the anterior part, and progressively show more posteriorward inclination towards the

posterior end of the blade. A prominent posteriorly pointing denticle is present in the posterior part of the blade. The basal cavity is situated at the posterior end of the blade and is rounded posteriorly and pointed anteriorly.'

It is considered here that the features described by Groessens are more consistent with the genus *Pelekysgnathus* than with *Spathognathodus*.

Early forms possess denticles behind the main cusp, but these are not present in later specimens (cf. Groessens 1971, pl. 1, figs. 2-4). The origin of the species is not clear.

Pe. bultyncki appears to have formed the stock from which both *Dollymae bouckaerti* and *Scaliognathus* developed. Expansion of the basal cavity and the development of nodes on the oral surface of the expansion seem to have led to *D. bouckaerti*. A range of forms showing this transition is available in sample HW 18 (slide LZA 6070). *Scaliognathus anchoralis* appears to have been derived by the development of lateral processes, the basal cavity remaining relatively restricted. *Bactrognathus* cf. *B. distortus* is considered to be a transitional form, with only one lateral process. In addition, the specimen of *Doliognathus* sp. (Pl. 58, figs. 17, 18) is close to *Pe. bultyncki* but has a single rudimentary lateral bar.

Material. 17 specimens, from 4 samples.

Pelekysgnathus sp. A Voges 1959

Plate 58, figs. 3-5

1959 *Pelekysgnathus* sp. A Voges, p. 287, pl. 33, fig. 44.

1971 ?*Pelekysgnathus* sp. A Voges; Groessens, pl. 2, fig. 3.

Remarks. Klapper (1966) has stated that this form, because of its double row of nodes, should be placed in the genus *Icriodus*. It has been retained in *Pelekysgnathus* for the present, however, until its relationship to other forms is understood. It appears to be related to *Pe. bultyncki*. In lateral view the two species are almost identical (see Pl. 58).

Material. 1 specimen.

Genus POLYGNATHUS Hinde 1879

Polygnathus communis Branson and Mehl 1934

Remarks. Hass (1959) subdivided *P. communis* on the basis of platform ornament. In the eastern Mendips the zonally important form *P. communis carina* Hass has been recovered, in addition to the long-ranging *P. communis communis* Branson and Mehl.

Immature specimens of this species have relatively large basal cavities and larger forms have relatively small cavities. The actual size of the basal cavity appears to remain constant throughout growth.

Polygnathus communis carina Hass 1959

Plate 59, figs. 10-13, 26

*1959 *Polygnathus communis* var. *carina* Hass, p. 391, pl. 47, figs. 8, 9.

- 1969 *Polygnathus communis dentatus* Druce, p. 95, pl. 18, figs. 13, 14.
 v1972 *Polygnathus communis carina* Hass; Matthews, Sadler, and Selwood, pp. 563-564, pl. 111, figs. 6, 7, 13 (with synonymy).

Remarks. Variants of *P. communis* showing the development of nodes or ridges on the anterior part of the platform or platform margin are placed within this subspecies.

Material. 162 specimens, from 16 samples.

Polygnathus communis communis Branson and Mehl 1934

Plate 59, figs. 8, 9, 15-17

- *1934 *Polygnathus communis* Branson and Mehl, p. 293, pl. 24, figs. 1-4.

Remarks. Some members of this subspecies have exceptionally long blades and abbreviated platforms. In these specimens the basal cavity often lies on the aboral surface in a position anterior to the blade-platform junction. These forms resemble *P. varcus* Stauffer.

Material. 455 specimens, from 55 samples.

Polygnathus inornatus Branson 1934

Plate 59, figs. 6, 7, 19, 20

- *1934 *Polygnathus inornata* Branson, p. 309, pl. 25, figs. 8, 26.
 1971 *Polygnathus inornatus* Branson; Klapper, p. 6 (with synonymy).

Remarks. Klapper (1971, p. 7) discussed the distinction between this species and *P. inornatus sensu* Branson and Mehl 1934. All specimens recovered from the Mendips lie within the range of variation of *P. inornatus* Branson, including forms which might previously have been called *P. lobatus* Branson and Mehl. The species is distinguished from *P. symmetricus* Branson by its well-defined subcircular basal cavity. In juvenile forms, the basal cavity resembles that of *P. communis*. A short free blade is common in this species.

Material. 151 specimens, from 9 samples.

The *Polygnathus symmetricus* Branson Group

Remarks. A number of polygnathids figured by other workers resemble *P. inornatus* in their platform development but differ in that they possess an elongate basal cavity. Klapper (1966) placed specimens with this type of cavity in *P. symmetricus* Branson, and his lead is followed here.

Within this group of polygnathids are recognized two subgroups. The first has been recovered from the lowest part of the Lower Limestone Shale Group seen at Maesbury and has been found in the Shirehampton Beds at Stoke Bishop (Bristol) by S. C. Matthews (pers. comm.). This subgroup closely resembles the specimens of *P. symmetricus* recovered from the Hannibal Shale by Branson and Mehl (1934) and is included within that species.

The second subgroup includes a broader range of polygnathids found higher up the stratigraphy, around the equivalent of the base of the *anchoralis*-Zone. These

were reported from Missouri by Thompson (1967) and Thompson and Fellows (1970). Some representatives are also available in the Avon Gorge (see Rhodes *et al.* 1969). These forms are included here as *P. cf. P. symmetricus*, since they have the characteristic basal cavity but are generally asymmetrical. This subgroup appears to develop from *Pseudopolygnathus multistriatus* by reduction of the size of the basal cavity and a change in the platform ornament. *Polygnathus nodomarginatus* Branson is considered to be a transitional form. Members of this subgroup show characteristic pseudopolygnathid asymmetry in juveniles, the platform on the right-hand side tending to be better developed than that on the left.

Juvenile forms of both subgroups have basal cavities which are deep and widely excavated along the underside of the platform, resembling those of spathognathodids.

Polygnathus nodomarginatus Branson 1934

Plate 57, figs. 2, 3

- *1934 *Polygnathus nodomarginata* Branson, p. 310, pl. 25, fig. 10.
- 1956 *Polygnathus nodomarginata* Branson; Bischoff and Ziegler, p. 156, pl. 12, fig. 6.
- 1956 *Polygnathus inornata* Branson; Bischoff and Ziegler, p. 157, pl. 12, fig. 5.
- v1969 *Pseudopolygnathus nodomarginatus* (Branson); Rhodes, Austin, and Druce, p. 212, pl. 9, figs. 1-4; pl. 12, figs. 6-8, 10.
- v. 1969 *Pseudopolygnathus cf. longiposticus* Branson and Mehl; Rhodes, Austin, and Druce, p. 210, pl. 30, figs. 11-16 (only).
- v. 1969 *Pseudopolygnathus triangulus cf. pinnatus* Voges; Rhodes, Austin, and Druce, p. 216, pl. 30, fig. 19.

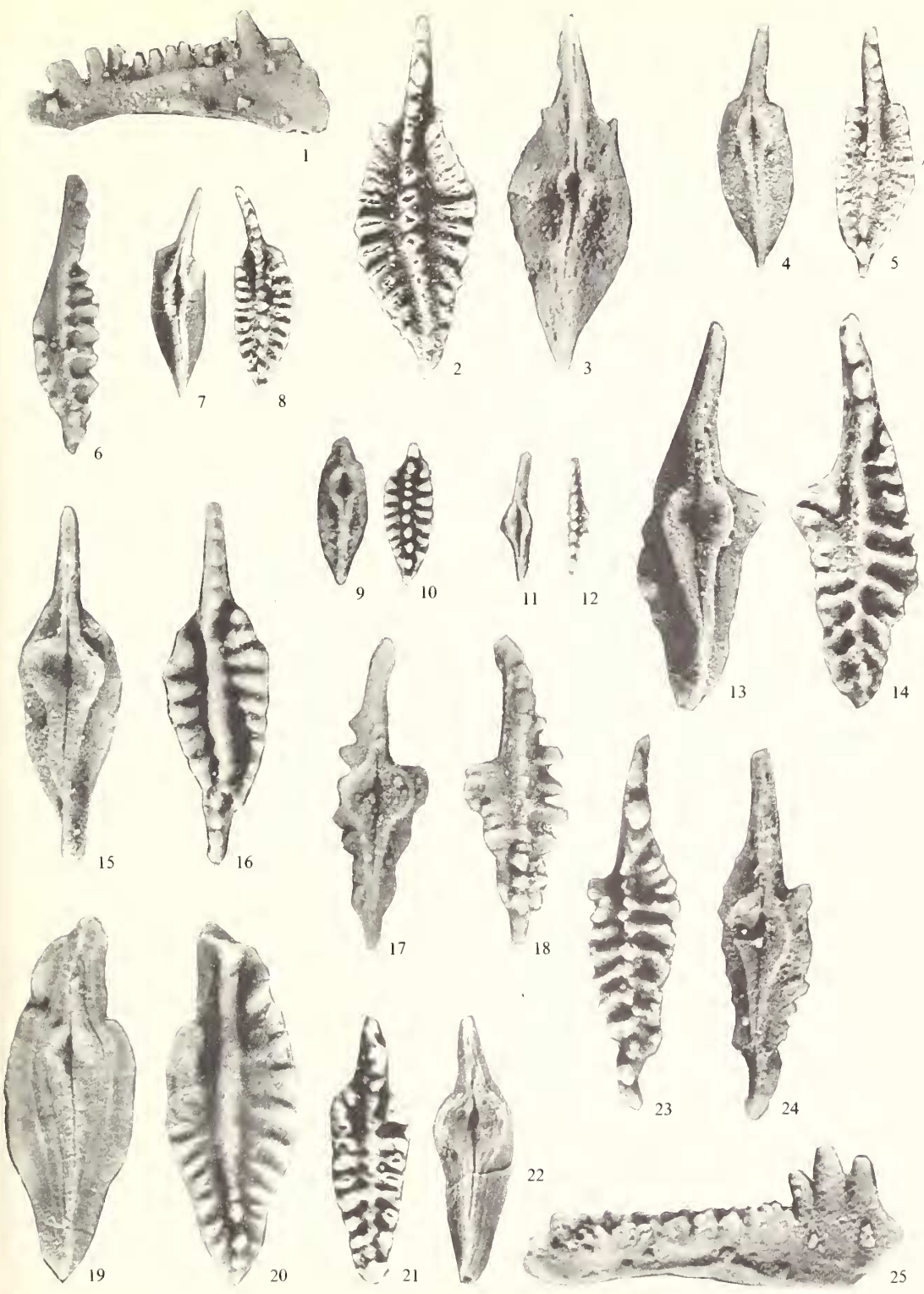
Remarks. This species is considered to be closely related to *Pseudopolygnathus multistriatus* Mehl and Thomas. The form appears briefly near the top of the range of *Ps. multistriatus* and some specimens have basal cavities similar to that of this pseudopolygnathid. The platform ornament is coarse, but polygnathid-like. Members of this species show a characteristic asymmetry, the right-hand side of the platform often extending farther anteriorly than the left.

Material. 3 specimens, from 3 samples.

EXPLANATION OF PLATE 57

Specimens dusted with ammonium chloride. All $\times 30$.

- Fig. 1. *Pseudopolygnathus postinodosus* Rhodes, Austin, and Druce. LZA 6052/1 (sample HW 2).
 Figs. 2, 3. *Polygnathus nodomarginatus* Branson. Oral and aboral views of LZA 6093/12 (HQ 15).
 Figs. 4, 5, 7, 8, 11, 12, 19, 20. *Polygnathus cf. P. symmetricus* Branson. 4, 5, Aboral and oral views of LZA 6098/11 (HQ 18). 7, 8, Aboral and oral views of LZA 6119/1 (HQ 36). 11, 12, Aboral and oral views of LZA 6118/6 (HQ 35). 19, 20, Aboral and oral views of LZA 6077/3 (HW 23).
 Figs. 6, 9, 10, 15, 16, 23-25. *Pseudopolygnathus multistriatus* Mehl and Thomas. 6, LZA 6046/9 (WH 17). 9, 10, Aboral and oral views of LZA 6100/2 (HQ 19). 15, 16, Aboral and oral views of LZA 6078/1 (HQ 1). 23, 24, 25, Oral, aboral, and lateral views of LZA 6047/2 (WH 18).
 Figs. 13, 14, 17, 18. *Pseudopolygnathus primus* Branson and Mehl. 13, 14, Aboral and oral views of LZA 6047/1 (WH 18). 17, 18, Aboral and oral views of LZA 6046/1 (WH 17).
 Figs. 21, 22. *Pseudopolygnathus dentilineatus* Branson. Oral and aboral views of LZA 6003/1 (Ma 2).



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Polygnathus symmetricus Branson 1934

Plate 59, figs. 22, 23

- *1934 *Polygnathus symmetrica* Branson, p. 310, pl. 25, fig. 11.
 1966 *Polygnathus symmetrica* Branson; Klapper, p. 21, pl. 4, figs. 7, 9; pl. 6, figs. 1, 5 (with synonymy).
 1968 *Polygnathus symmetrica* Branson; Straka, p. 35, pl. 1, figs. 6, 9 (only).

Remarks. This species is common at the base of the Lower Limestone Shale Group in the Mendips. Immature forms have a basal cavity which is spathognathodid-like, underlying the entire platform, and a symmetrical platform.

Material. 68 specimens, from 5 samples.

Polygnathus cf. *P. symmetricus* Branson 1934

Plate 57, figs. 4, 5, 7, 8, 11, 12, 19, 20

The following are regarded as falling within this subgroup:

- 1967 *Polygnathus mehli* Thompson, p. 47, pl. 2, figs. 1-6.
 1969 *Polygnathus bischoffi* Rhodes, Austin, and Druce, p. 184, pl. 13, figs. 8-11.
 1969 *Polygnathus lacinatus asymmetricus* Rhodes, Austin, and Druce, p. 188, pl. 11, figs. 1-4.
 1969 *Polygnathus lacinatus circaperipherus* Rhodes, Austin, and Druce, p. 189, pl. 11, figs. 12-15.
 1969 *Polygnathus lacinatus lacinatus* Huddle; Rhodes, Austin, and Druce, p. 189, pl. 11, figs. 8-10.
 1969 *Polygnathus lacinatus prelobatus* Rhodes, Austin, and Druce, p. 190, pl. 11, figs. 5-7, 11.
 1970 *Polygnathus bischoffi* Rhodes, Austin, and Druce; Marks and Wensink, p. 268, pl. 1, fig. 18.

Remarks. Included in this subgroup are all those 'late' polygnathids having a narrow platform and elongate basal cavity. Immature members of this species have spathognathodid-like basal cavities, similar to those seen in *P. symmetricus*. The platform in immature forms is, however, often asymmetrical, with the right-hand side consistently better developed than the left (see Pl. 57, fig. 12).

The subgroup appears to develop from *Pseudopolygnathus multistriatus*, and forms with basal cavities resembling those of this pseudopolygnathid are found.

Material. 217 specimens, from 39 samples.

Genus PSEUDOPOLYGNATHUS Branson and Mehl 1934

Pseudopolygnathus dentilineatus Branson 1934

Plate 57, figs. 21, 22

- *1934 *Pseudopolygnathus dentilineata* Branson, p. 317, pl. 26, fig. 22.
 1966 *Pseudopolygnathus dentilineata* Branson; Klapper, p. 14, pl. 5, figs. 10, 11 (with synonymy).
 v. 1969 *Pseudopolygnathus expansus* Rhodes, Austin, and Druce, p. 209, pl. 5, figs. 2, 4.
 v. 1969 *Pseudopolygnathus vogesi* Rhodes, Austin, and Druce, p. 216, pl. 5, figs. 1, 3, 5-8.
 1970 *Pseudopolygnathus dentilineatus* Branson; Thompson and Fellows, p. 99, pl. 5, figs. 1, 5.

Remarks. As suggested by Klapper (1966, p. 15), *Ps. dentilineatus* is characterized by a basal cavity which, in mature specimens, is as wide as the platform. The basal cavity tends to be subcircular and widely flared, and is therefore distinct from that of *Ps. multistriatus*, which is narrow and attenuate posteriorly.

Material. 7 specimens, from 2 samples.

Pseudopolygnathus multistriatus Mehl and Thomas 1947

Plate 57, figs. 6, 9, 10, 15, 16, 23-25

- *1947 *Pseudopolygnathus multistriata* Mehl and Thomas, p. 16, pl. 1, fig. 36.
 1967 *Pseudopolygnathus multistriata* Mehl and Thomas; Thompson, p. 49, pl. 4, figs. 15, 16, 19, 20 (with synonymy).
 1968 *Pseudopolygnathus multistriata* Mehl and Thomas; Canis, p. 547, pl. 73, figs. 13, 16.
 v1969 *Pseudopolygnathus multistriatus* Mehl and Thomas; Rhodes, Austin, and Druce, p. 211, pl. 5, figs. 14-16; pl. 6, fig. 2.
 v. 1969 *Pseudopolygnathus dentilineatus* Branson; Rhodes, Austin, and Druce, p. 208, pl. 5, figs. 9-13; pl. 6, fig. 8.
 v. 1969 *Pseudopolygnathus primus* Branson and Mehl; Rhodes, Austin, and Druce, p. 214, pl. 6, figs. 4, 5, 7, 11, 12 (only).

Remarks. Mature specimens of this form possess an elongate basal cavity which is not as wide as the platform. Late forms may have a much-reduced basal cavity. Hass (1959, pl. 47) figured an ontogenetic series of *Ps. lanceolata* (now placed in synonymy with *Ps. multistriatus*). Specimens found during the present study conform to this series, certain immature forms having nodes on the right-hand side only, and resembling *Spathognathodus aculeatus* (Branson and Mehl). Members of this species are again more fully developed on the right-hand side. The basal cavity may be relatively large in immature specimens. In certain forms the blade does not continue into the carina on the platform, but tends towards the nodes on the right-hand side of the platform (see Pl. 57, fig. 23). These forms bear some resemblance to the genus *Clydagnathus* Rhodes, Austin, and Druce.

Material. 73 specimens, from 25 samples.

Pseudopolygnathus postinodosus Rhodes, Austin, and Druce 1969

Plate 57, fig. 1

- v*1969 *Pseudopolygnathus postinodosus* Rhodes, Austin, and Druce, p. 213, pl. 6, fig. 6.

Remarks. This form lacks a platform, but the lateral view is similar to that of *Ps. multistriatus* (compare Pl. 57, fig. 1 with Pl. 57, fig. 25).

Material. 1 specimen.

Pseudopolygnathus primus Branson and Mehl 1934

Plate 57, figs. 13, 14, 17, 18

- *1934 *Pseudopolygnathus prima* Branson and Mehl, p. 298, pl. 24, figs. 24, 25.
 v1969 *Pseudopolygnathus primus* Branson and Mehl; Rhodes, Austin, and Druce, p. 214, pl. 6, fig. 10 (only).
 1970 *Pseudopolygnathus primus* Branson and Mehl; Thompson and Fellows, p. 101, pl. 5, figs. 15, 16, 18, 19 (with synonymy).

Remarks. The characteristics of this species are taken as follows: The platform possesses a pronounced lateral lobe on either the inner or outer side, separated from the carina by a depression. The basal cavity is not as wide as the platform in mature forms. Immature forms again show a more fully developed right-hand side, irrespective of whether this is the inner or outer side. As Klapper (1966, p. 14) has

pointed out, some specimens of *Ps. primus* resemble *Ps. triangulus pinnatus* Voges (see Pl. 57, fig. 18). This latter species possesses a smaller basal cavity, and tends to have a broad, flat platform.

Material. 6 specimens, from 3 samples.

Pseudopolygnathus triangulus Voges 1959
Pseudopolygnathus triangulus pinnatus Voges 1959

Plate 58, figs. 23, 24, 27, 28, 30, 31, 33, 34

- *1959 *Pseudopolygnathus triangula pinnata* Voges, p. 302, pl. 34, figs. 59–66.
- 1964 *Pseudopolygnathus triangula pinnata* Voges; Higgins, Wagner-Gentis, and Wagner, pl. 4, fig. 16.
- 1967 *Pseudopolygnathus triangula pinnata* Voges; Boogaert, p. 285, pl. 3, figs. 9, 10 (with synonymy).
- 1969 *Pseudopolygnathus triangula pinnata* Voges; Matthews (1969a), p. 271, pl. 48, figs. 3, 4, 8, 10, 11.
- 1969 *Pseudopolygnathus triangula pinnata* Voges; Matthews (1969b), pl. 51, fig. 8.
- non v1969 *Pseudopolygnathus triangulus* cf. *pinnatus* Voges; Rhodes, Austin, and Druce, p. 216, pl. 30, fig. 19 (= *Polygnathus nodomarginatus* Branson).
- 1970 *Pseudopolygnathus triangulus pinnatus* Voges; Marks and Wensink, p. 269, pl. 1, fig. 17.
- 1970 *Pseudopolygnathus triangulus pinnatus* Voges; Thompson and Fellows, p. 102, pl. 6, figs. 6, 11, 12.

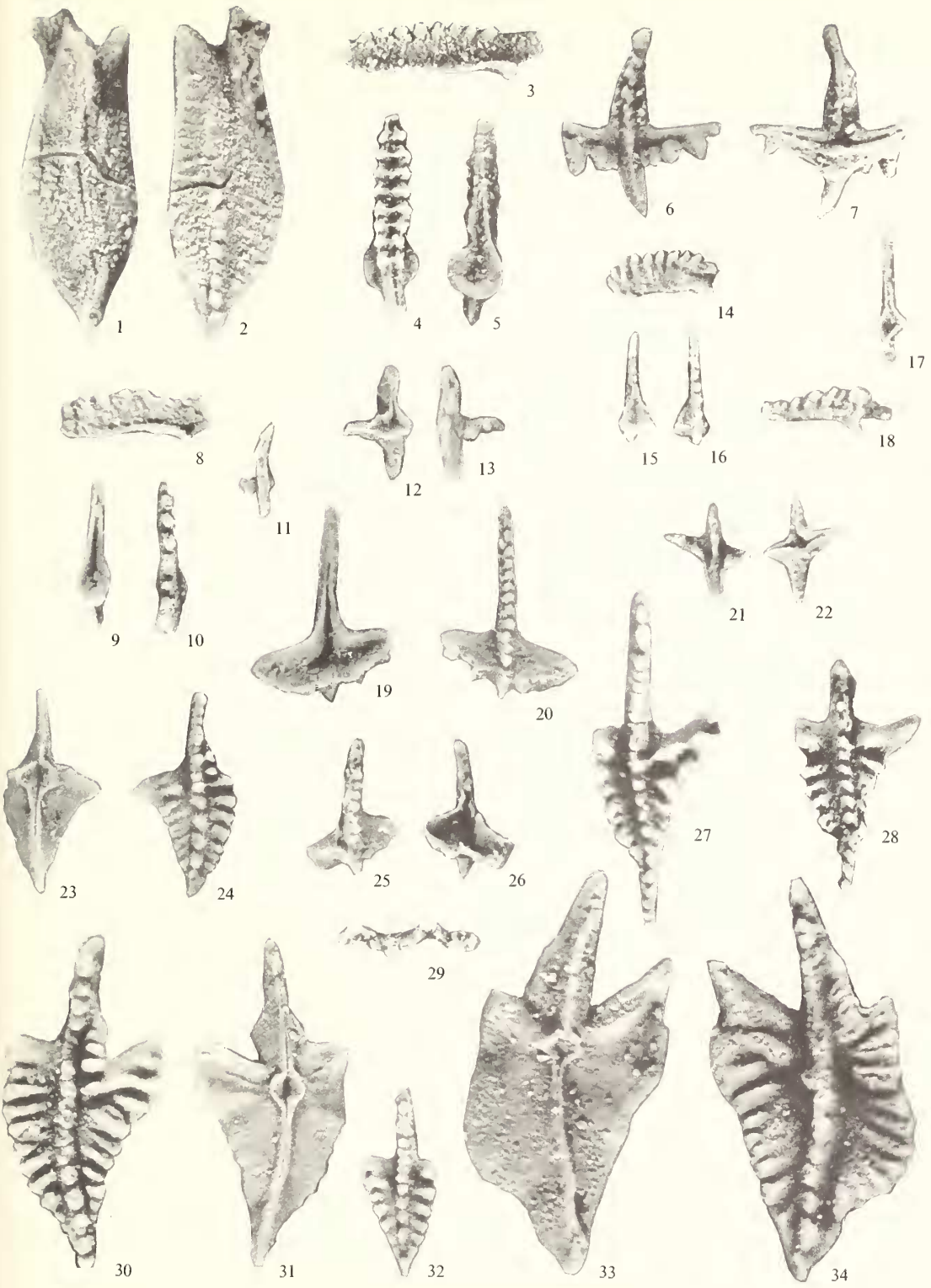
Remarks. Specimens found during the present study show a similar range of variation to that illustrated by Voges (1959). Members of this subspecies again show the tendency for the right-hand side to be more fully developed than the left. A row of platform denticles is often present extending along the blade towards the anterior on the right-hand side, regardless of which side includes the pinnation (compare Pl. 58, fig. 30 with Pl. 58, fig. 34).

Material. 65 specimens, from 14 samples.

EXPLANATION OF PLATE 58

Specimens dusted with ammonium chloride. All $\times 30$.

- Figs. 1, 2. *Mestognathus beckmanni* Bischoff. Aboral and oral views of LZA 6135/1 (sample HQ 76).
- Figs. 3–5. *Pelekysgnathus* sp. A Voges 1959. Lateral, oral, and aboral views of LZA 6150/2 (Va 13).
- Figs. 6, 7, 21, 22. *Scaliognathus anchoralis* Branson and Mehl. 6, 7, Oral and aboral views of LZA 6104/2 (HQ 22). 21, 22, Oral and aboral views of LZA 6093/11 (HQ 15).
- Figs. 8–10, 14–16. *Pelekysgnathus bultyncki* (Groessens). 8–10, Lateral, aboral, and oral views of LZA 6078/2 (HQ 1). 14–16, Lateral, aboral, and oral views of LZA 6068/6 (HW 18).
- Figs. 11–13. *Bactrognathus* cf. *B. distortus* Branson and Mehl. 11, LZA 6092/1 (HQ 14a): specimen later accidentally destroyed. 12, 13, Aboral and oral views of LZA 6075/1 (HW 21).
- Figs. 17, 18. *Doliognathus* sp. Aboral and oblique lateral/oral views of LZA 6068/3 (HW 18).
- Figs. 19, 20, 25, 26. *Dollymae bouckaerti* Groessens. 19, 20, Aboral and oral views of LZA 6068/11 (HW 18). 25, 26, Oral and aboral views of LZA 6068/8 (HW 18).
- Figs. 23, 24, 27, 28, 30, 31, 33, 34. *Pseudopolygnathus triangulus pinnatus* Voges. 23, 24, Aboral and oral views of LZA 6077/2 (HW 23). 27, LZA 6104/1 (HQ 22). 28, LZA 6106/1 (HQ 23). 30, 31, Oral and aboral views of LZA 6077/1 (HW 23). 33, 34, Aboral and oral views of LZA 6098/2 (HQ 18).
- Fig. 29. *Hindeodella segaformis* Bischoff. LZA 6129/1 (HQ 46).
- Fig. 32. *Pseudopolygnathus triangulus triangulus* Voges. LZA 6111/1 (HQ 28).



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Pseudopolygnathus triangulus triangulus Voges 1959

Plate 58, fig. 32

- *1959 *Pseudopolygnathus triangula triangula* Voges, p. 304, pl. 35, figs. 7-13.
 1969 *Pseudopolygnathus triangula triangula* Voges; Matthews (1969a), p. 271, pl. 48, figs. 2, 7.
 1970 *Pseudopolygnathus triangulus triangulus* Voges; Thompson and Fellows, p. 103, pl. 7, figs. 6, 7 (with synonymy).

Remarks. Specimens recovered are similar to those figured by Voges (1959, pl. 35). Voges (1959, table 1) gave this subspecies a lower range than that of *Ps. triangulus pinnatus*. In the eastern Mendips the two forms have almost identical ranges.

Material. 8 specimens (including 2 cf. determinations), from 6 samples.

Genus SCALIOGNATHUS Branson and Mehl 1941

Scaliognathus anchoralis Branson and Mehl 1941

Plate 58, figs. 6, 7, 21, 22

- *1941 *Scaliognathus anchoralis* Branson and Mehl, p. 102, pl. 19, figs. 29-32.
 1964 *Scaliognathus anchoralis* Branson and Mehl; Burton, range-chart, facing p. 74.
 1967 *Scaliognathus anchoralis* Branson and Mehl; Zikmundová, pl. 1, figs. 1, 2, 4.
 1968 *Scaliognathus anchoralis* Branson and Mehl; Schulze, p. 220, pl. 20, fig. 32 (with synonymy).
 1969 *Scaliognathus anchoralis* Branson and Mehl; Matthews (1969a), p. 272, pl. 49, figs. 1-10.
 1969 *Scaliognathus anchoralis* Branson and Mehl; Matthews (1969b), pl. 51, figs. 1, 2.
 1970 *Scaliognathus anchoralis* Branson and Mehl; Marks and Wensink, p. 269, pl. 4, fig. 12.
 1970 *Scaliognathus anchoralis* Branson and Mehl; Thompson and Fellows, p. 103 (with additional synonymy).
 1971 *Scaliognathus anchoralis* Branson and Mehl; Groessens, pl. 1, figs. 9, 10.

Remarks. The species is one of the indices of the German *anchoralis*-Zone. It has, in the past, been reported mainly from 'basinal' sequences, and there have been suggestions (e.g. Rhodes *et al.* 1969, p. 65) that facies-control resulted in virtual exclusion of this species from the 'shelf' limestone successions. It now seems clear that the species is present in the limestone sequences and that its absence at many places is due in part to discontinuities within the successions.

The species appears to have developed from *Pelekysgnathus bultyncki* (Groessens) by the development of lateral processes at the posterior end (see discussion under *Pe. bultyncki*, above).

Material. 7 specimens, from 5 samples.

Genus SIPHONODELLA Branson and Mehl 1944

Remarks. The suggestions put forward by Klapper (1971) on the systematic palaeontology of this genus are accepted here.

Siphonodella cooperi Hass 1959

Plate 59, figs. 39, 40

- *1959 *Siphonodella cooperi* Hass, p. 392, pl. 49, figs. 35, 36.
 1971 *Siphonodella cooperi* Hass; Klapper, p. 10, pl. 1, figs. 13-15; pl. 2, figs. 1-3 (with synonymy).

Remarks. This species is distinguished from *S. isosticha* (Cooper) by the ornament of transverse ridges on the outer side of the platform. Most specimens of *S. isosticha* also show faint ridges on the outer side, but some are considered to be sufficiently well developed in this respect to justify inclusion within *S. cooperi*.

Material. 3 specimens, from 2 samples.

Siphonodella cf. *crenulata* (Cooper 1939)

Plate 59, figs. 36, 37

Remarks. Matthews and Butler (in press) discuss occurrences of siphonodellids with platform outlines resembling those of *S. crenulata* (Cooper), but without the characteristic ornament of this species.

Material. 2 specimens, from 1 sample.

Siphonodella isosticha (Cooper 1939)

Plate 59, figs. 21, 30, 31

*1939 *Siphonognathus isosticha* Cooper, p. 409, pl. 41, figs. 9, 10.

1971 *Siphonodella isosticha* (Cooper); Klapper, p. 10, pl. 1, fig. 16 (with synonymy).

Remarks. Klapper (1971, p. 10) made clear the definition of *Siphonodella isosticha* and reillustrated Cooper's holotype. In this species the longest rostral ridge terminates at the outer margin. The inner platform is weakly nodose and the outer margin may be unornamented or have weak transverse ridges. This redefinition makes it clear that *Siphonodella cooperi hassi* Thompson and Fellows is synonymous with *S. isosticha*.

Material. 21 specimens, from 6 samples.

Siphonodella cf. *S. isosticha* (Cooper 1939)

Plate 59, fig. 38

1971 *Siphonodella* cf. *S. isosticha* (Cooper); Klapper, p. 12, pl. 1, figs. 17-20 (with synonymy).

Remarks. Klapper (1971, p. 12) applied this name to those siphonodellids with weak ornament but with rostral ridges terminating on the platform without reaching the margin.

Material. 5 specimens, from 3 samples.

Siphonodella obsoleta Hass 1959

Plate 59, figs. 33, 34

*1959 *Siphonodella obsoleta* Hass, p. 392, pl. 47, figs. 1, 2.

1971 *Siphonodella obsoleta* Hass; Klapper, p. 12, pl. 1, fig. 25 (with synonymy).

v1972 *Siphonodella obsoleta* Hass; Matthews, Sadler, and Selwood, p. 565, pl. 111, figs. 4, 5 (with additional synonymy).

Remarks. This species is characterized by the presence of a long outer rostral ridge, extending to the posterior part of the platform before meeting the margin. The

platform is relatively long and narrow. As Klapper (1971, p. 12) has pointed out, the species may have more than two rostral ridges. Certain specimens here have an additional ridge (see Pl. 59, fig. 33).

Material. 15 specimens, from 5 samples.

Genus SPATHOGNATHODUS Branson and Mehl 1941
Spathognathodus aculeatus (Branson and Mehl 1934)

*1934 *Spathodus aculeatus* Branson and Mehl, p. 186, pl. 17, figs. 11, 14.

Remarks. Matthews (in Matthews and Naylor 1973) gives full systematic treatment to this species. Specimens recovered during the present study are not well enough preserved or numerous enough to justify lengthy discussion.

Material. 4 specimens, from 2 samples.

Spathognathodus crassidentatus (Branson and Mehl 1934)

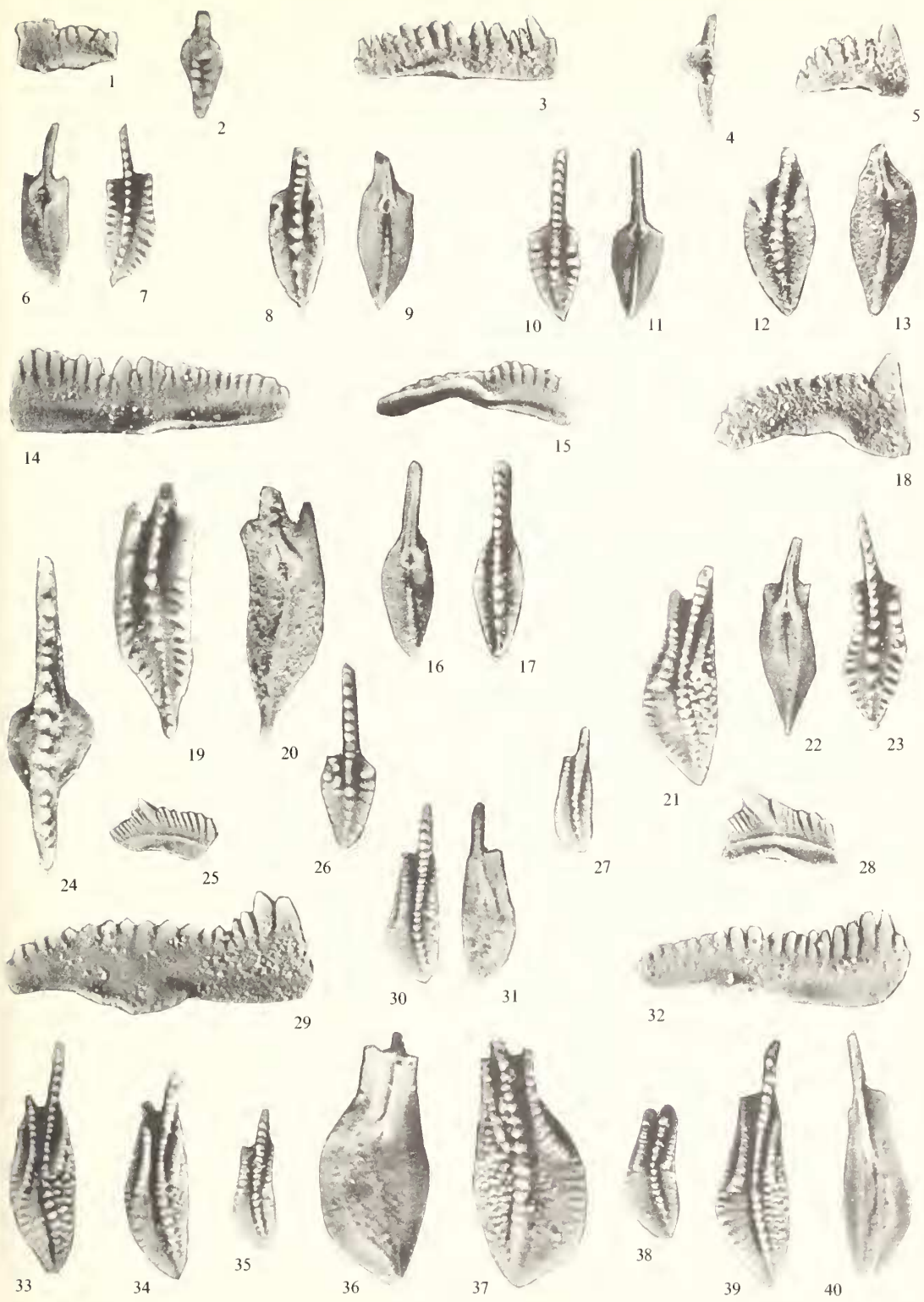
Plate 59, figs. 18, 24, 29

- *1934 *Spathodus crassidentatus* Branson and Mehl, p. 276, pl. 22, fig. 17.
1966 *Spathognathodus crassidentatus* (Branson and Mehl); Klapper, p. 23, pl. 5, figs. 15-17 (with synonymy).
1970 *Spathognathodus crassidentatus* (Branson and Mehl); Thompson and Fellows, p. 111, pl. 7, figs. 8, 14.

EXPLANATION OF PLATE 59

Specimens dusted with ammonium chloride. All $\times 30$.

- Figs. 1, 2. *Patrognathus variabilis* Rhodes, Austin, and Druce. Lateral and oral views of LZA 6005/2 (sample Ma 4).
Figs. 3, 14, 32. *Spathognathodus stabilis* (Branson and Mehl). 3, LZA 6150/3 (Va 13). 14, LZA 6104/3 (HQ 22). 32, LZA 6118/3 (HQ 35): variant approaching *S. crassidentatus*.
Figs. 4, 5. *Spathognathodus scitulus* (Hinde). Aboral and lateral views of LZA 6129/2 (HQ 46).
Figs. 6, 7, 19, 20. *Polygnathus inornatus* Branson. 6, 7, Aboral and oral views of LZA 6019/8 (Ma 19). 19, 20, Oral and aboral views of LZA 6012/2 (Ma 11).
Figs. 8, 9, 15-17. *Polygnathus communis communis* Branson and Mehl. 8, 9, Oral and aboral views of LZA 6019/11 (Ma 19). 15-17, Lateral, aboral, and oral views of LZA 6100/3 (HQ 19).
Figs. 10-13, 26. *Polygnathus communis carina* Hass. 10, 11, Oral and aboral views of LZA 6083/4 (HQ 7). 12, 13, Oral and aboral views of LZA 6083/3 (HQ 7). 26, LZA 6083/1 (HQ 7).
Figs. 18, 24, 29. *Spathognathodus crassidentatus* (Branson and Mehl). 18, LZA 6098/3 (HQ 18). 24, 29, Oral and lateral views of LZA 6086/2 (HQ 10).
Figs. 21, 30, 31. *Siphonodella isosticha* (Cooper). 21, LZA 6019/3 (Ma 19). 30, 31, Oral and aboral views of LZA 6019/1 (Ma 19).
Figs. 22, 23. *Polygnathus symmetricus* Branson. Aboral and oral views of LZA 6005/1 (Ma 4).
Figs. 25, 28. *Elictognathus laceratus* (Branson and Mehl). 25, LZA 6019/12 (Ma 19). 28, LZA 6019/13 (Ma 19).
Figs. 27, 35. *Siphonodella* sp. (juv?). 27, LZA 6019/7 (Ma 19). 35, LZA 6019/4 (Ma 19).
Figs. 33, 34. *Siphonodella obsoleta* Hass. 33, LZA 6019/2 (Ma 19). 34, LZA 6014/1 (Ma 15).
Figs. 36, 37. *Siphonodella* cf. *crenulata*. Aboral and oral views of LZA 6012/1 (Ma 11).
Fig. 38. *Siphonodella* cf. *S. isosticha*. LZA 6019/5 (Ma 19).
Figs. 39, 40. *Siphonodella cooperi* Hass. Oral and aboral views of LZA 6019/6 (Ma 19).



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Remarks. This species was restricted by Klapper (1966, p. 23) to those forms having two main denticles at the anterior end of the blade and a slightly arched profile. Specimens with a similar profile but a single major anterior denticle are also included in the species here (see Pl. 59, fig. 18). A fuller synonymy list is available in Matthews (in Matthews and Naylor 1973).

Material. 40 specimens, from 20 samples.

Spathognathodus scitulus (Hinde 1900)

Plate 59, figs. 4, 5

- *1900 *Polygnathus scitulus* Hinde, p. 343, pl. 9, figs. 9–11 (only).
- 1963 *Spathognathodus scitulus* (Hinde); Rexroad and Collinson, p. 20, pl. 2, figs. 14, 19, 29–31 (with synonymy).
- v1969 *Spathognathodus scitulus* (Hinde); Rhodes, Austin, and Druce, p. 232, pl. 8, figs. 9–11.

Remarks. This spathognathodid has a distinctively flared basal cavity on the outer side. Few denticles are present and these expand rapidly in size from the posterior end to the anterior. In some specimens one or two ridges develop on the oral surface of the flared cavity.

Material. 11 specimens, from 6 samples.

Spathognathodus stabilis (Branson and Mehl 1934)

Plate 59, figs. 3, 14, 32

- *1934 *Spathodus stabilis* Branson and Mehl, p. 188, pl. 17, fig. 20.

Remarks. Matthews (in Matthews and Naylor 1973) supplies a full description and synonymy list for this species, and no attempt will be made to duplicate this here. Specimens similar to that illustrated as *Spathognathodus* sp. A by Groessens (1971, pl. 2, fig. 7) occur in many samples from *anchoralis*-Zone levels in the Mendips. They are considered to lie within the range of variation of *Sp. stabilis*.

Material. 174 specimens, from 49 samples.

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APPENDIX

List of conodont faunas from isolated Lower Limestone Shale Group samples. ($\frac{1}{2}$ -kg samples processed.)

1. The Palate Bed, from the Avon Gorge (ST 555 746): ?*Elictognathus* sp. (3 specimens), *Clydagnathus* spp. (10), *Patrognathus variabilis* Rhodes, Austin, and Druce (3), *Polygnathus inornatus* Branson (33), *P. scobiniformis* Branson (4), *Pseudopolygnathus dentilineatus* Branson (7), *Siphonodella duplicata* (Branson and Mehl) (3), *Spathognathodus plumulus* Rhodes, Austin, and Druce (11), *Sp. stabilis* Branson and Mehl (1), Bars (24). Slide LZA 6161.
2. Phosphatic lag deposit on Clevedon Foreshore (ST 402 718): *Clydagnathus* sp. (2), *Patrognathus variabilis* Rhodes, Austin, and Druce (1), *Polygnathus inornatus* Branson (8), *Pseudopolygnathus dentilineatus* Branson (1), *Spathognathodus plumulus* Rhodes, Austin, and Druce (1), Bars (10). Slide LZA 6164.
3. Bed with *Vaughania* on Portishead Foreshore (ST 465 775): *Spathognathodus plumulus* Rhodes, Austin, and Druce (3). Slide LZA 6165.
4. Small quarry north of road at Asham (ST 717 463). Oolite: *Patrognathus variabilis* Rhodes, Austin, and Druce (2), *Polygnathus symmetricus* Branson (20), *Pseudopolygnathus dentilineatus* Branson (4), *Spathognathodus stabilis* Branson and Mehl (1), Bars (15). Slide LZA 6162.
5. Sample from stream section at Asham (ST 717 464): *Pseudopolygnathus dentilineatus* Branson (2), Bars (2). Slide LZA 6163.